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CONTENTS.

PAGE

No. 1. — The Early Development of Asplanchna Herrickii de Guerne; a contribution to Developmental Mechanics. By H. S. JENNINGS. (10 Plates.) October, 1896 1

No. 2. — Some Variations in the Genus Eucope. By A. AGASSIZ and W. M. WOODWORTH. (9 Plates.) November, 1896 119

No. 3. — Reports on the Results of Dredging in the "Blake." XXXVII. Supplementary Notes on the Crustacea. By W. FAXON. (2 Plates.) November, 1896 151

No. 4. — On the Colors and Color-patterns of Moths and Butterflies. By A. G. MAYER. (10 Plates). February, 1897 167

No. 5. — The Mesenteries and Siphonoglyphs in Metridium marginatum Milne Edwards. By G. H. PARKER. (1 Plate.) March, 1897 257

No. 6. — Photomechanical changes in the Retinal Pigment Cells of Palaemonetes and their relation to the central nervous system. By G. H. PARKER. (1 Plate.) April, 1897 273

No. 1. — *The Early Development of Asplanchna Herrickii de Guerne. A Contribution to Developmental Mechanics.*[1] By HERBERT S. JENNINGS.

CONTENTS.

PAGE

Introduction 2
Part First. Developmental Mechanics . 4
- I. Statement of Problems 4
  - 1. Cleavage 4
    - A. Direction of Cleavage 4
      - (1) Berthold's principle of least surfaces 4
      - (2) Hertwig's law of the spindle in the longest axis of the protoplasmic mass 5
      - (3) Braem's theory of separation in the direction of least resistance 5
      - (4) Roux's theory of a compromise between the tendency immanent in the nucleus and the tendency due to the form of the protoplasmic mass . . . 6
      - (5) Heidenhain's problem of a definite angle of rotation . . . 6
      - (6) Sachs's law of the right-angled arrangement of cell walls . . 7
      - (7) Rauber's theory of inter-attraction of asters 7
      - (8) Braem's principle of equal resistance at the two ends of the spindle 7
    - B. Equality or Inequality of Cleavage 7
    - C. Rate of Cleavage 8
    - D. Differentiation during Cleavage . 9
  - 2. Later Developmental Processes . 9
- II. Descriptive Portion 10
  - 1. Form and Structure of the Egg . 10

PAGE

  - 2. Maturation 12
  - 3. Orientation of the Developing Embryo 14
  - 4. Cleavage 16
    - Nomenclature 16
    - First Cleavage 18
    - Second " 20
    - Third " 22
    - Fourth " 24
    - Fifth " 29
    - Sixth " 35
    - Seventh and Later Cleavages . 45
      - The Ectoderm 45
      - The Entoderm 54
- III. Discussion of the Bearing of the Observations on the Problems . 58
  - 1. Cleavage 58
    - A. Direction of Cleavage 58
      - (1) Berthold's theory of least surfaces 58
      - (2) Hertwig's law of the spindle in the long axis 60
      - (3) Braem's theory of least resistance 69
      - (4) Roux's theory 70
      - (5) Heidenhain's problem of a definite angle of rotation . . . 72
      - (6) Sachs's law of the right-angled arrangement of cell walls . . 73
      - (7) Rauber's theory of the inter-attraction of asters 74
      - (8) Braem's principle of equal resistance at the two ends of the spindle 74

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. LXX.

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PAGE
B. Equality or Inequality of Cleavage Products 74
C. Rate of Cleavage 74
D. Differentiations accompanying Cleavage 77
2. Gastrulation 80
3. General Considerations 83
Part Second. Discussion of Matters bearing upon the Morphology of the Rotifera 87
1. Previous Knowledge of Asplanchna Herrickii 88
2. Development 89
A. Maturation 89
B. Cleavage 94
C. Summary on Maturation and Cleavage in the Rotifera . . 100
Part Third. Material and Methods . . 101
General Summary 106
A. Observations 106
B. Conclusions 108
Literature Cited 111
Explanation of Plates 117

INTRODUCTION.

The following pages contain a study of the early development of an organism, with especial reference to recent theories in regard to the laws of cleavage and the relation of cleavage to morphogenesis.

Many theories and so called laws have been set forth concerning the factors determining the manner and rate of cleavage. These have taken the form chiefly of theories in regard to the causes of the *direction of the spindle,* of the *equality* or *inequality* in size of the products of division, and of the *relative rapidity* with which the different cleavage cells divide. Yet few attempts have been made to interpret consistently the cleavage of any given organism with relation to any or all of these theories. The sketch of Braem ('94) with regard to the Echinoderm egg, and the recent studies of Ziegler ('95) and zur Strassen ('96)[1] on the Nematode egg, are almost the only works that can be cited in which an attempt has been made to show the relation of any theory or theories to the series of normal cleavages in any animal. In other discussions the theories have been based upon experimental evidence or upon scattered observations. Yet it is, of course, the *normal processes* for which explanations are desired; scattered observations may be adduced for almost any view. It seems of the greatest importance, therefore, to show clearly the exact relation which the theories hitherto proposed have to the actual series of cell divisions in the development of particular organisms.

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[1] In view of the close similarity of some of my conclusions with some of those in the more recent ('96) of two papers by zur Strassen, it may be proper to state that a copy of the present paper, exactly as here published, with the exception of some verbal alterations and the addition of a few references, was deposited with the Faculty of Arts and Sciences of Harvard University on April 30, 1896, while zur Strassen's ('96) paper was not received here till May 13.

Furthermore, there is much discussion of the question as to whether cleavage is a mere quantitative separation of a single mass into smaller masses similar in nature to each other and to the original egg, or whether it is accompanied by a differentiation of the separated blastomeres, — as a result either of qualitative division or other changes.

A third question of theoretical interest, somewhat related to the last, is whether the method of cleavage has a direct mechanical relation to future morphogenetic processes, or whether it is merely the passing of partitions through a mass of protoplasm, the order in which this occurs and the arrangement of the partitions being immaterial. For example, Is gastrulation a process independent of cleavage and merely requiring the latter as a prerequisite, — as the planting of seeds must be preceded by ploughing, — or is gastrulation in some way connected with or dependent upon the manner of cleavage? Stated in the most general terms, this is the question: Is cell division a *direct* morphogenetic factor, or are the real formative processes dependent upon the introduction of other factors after the cleavage is finished?

With these questions in mind, I have studied the development of an organism of the class Rotifera throughout those stages of development in which it is possible to make the *cells* the units of observation, — that is, through cleavage and gastrulation and somewhat later.

Broadly stated, the object of the work may be expressed as *the analysis of the early development of an organism into the simplest factors possible.*

The development of Asplanchna Herrickii has not been studied previously, and in the course of this paper it will be necessary to discuss some matters which are of importance primarily to persons who are engaged particularly with the morphology of the Rotifera, and which are not of especial interest from a morphogenetic standpoint. In order to distinguish these two lines of discussion, I shall divide the work into two main portions. Part First will contain all matters bearing upon developmental mechanics. Here will be found the minute description of the cleavage, gastrulation, and other processes, as well as a discussion of their bearing upon the problems of morphogenesis. Part Second will contain a brief review of previous knowledge of the organism studied, a comparison of the development, so far as traced, with the development of other Rotifera, and a discussion of some of the conditions described by other authors. These principal parts will be followed by a third, on material, methods, and other subordinate matters, and the whole will be closed by a summary of the more important conclusions arrived at.

PART FIRST. — DEVELOPMENTAL MECHANICS.

I. Statement of Problems.

We shall deal in the following pages with (1) cleavage, (2) gastrulation, and (3) the relation of these to each other.

1. Cleavage.

It will be necessary, in studying the cleavage and the factors determining it, to enter into minute details as to the movements of asters, the form and dimensions of cells, and other similar matters; the effort of following this, in itself somewhat laborious, description will be much lightened by holding in mind the problems upon which it bears. I shall therefore give first a statement of the main theories which have been advanced as to the determining factors in cell division.

Cell division presents three aspects, in each of which its nature is in some way determined. (A) As to the *direction* of cleavage: the position in which the new septum is to appear. Since this bears a definite relation, in general, to the position of the spindle leading to the cleavage, we may speak of this aspect as the determination of the direction of the spindle. (B) As to the *relative size* of the two products; whether the division is equal or unequal. (C) As to the relative *time* of division, or the interval between successive cleavages.

Besides these, we have (D) the question of the *qualitative* nature of cleavage. Are all the cells that are produced of similar structural and material character, or is cleavage accompanied by qualitative differentiation of the blastomeres, — either as a result of qualitative karyokinesis or otherwise?

A. *Theories as to the Factors determining the Direction of the Spindle and the Position of the new Cell Wall.*

The theories as to the factors determining the direction of cleavage are numerous, and have been much discussed of late. General reviews of these theories will be found in Driesch ('92, p. 26), Braem ('94, p. 340), Ziegler ('94, p. 136), and McMurrich ('95). I shall give here as brief and precise a statement of each theory as possible, first in my own words, then, so far as practicable, in a quotation from the author.

(1) *Berthold's principle of least surfaces.* — Berthold ('86) holds that the form and relative position of cells, and as a consequence their direc-

tion of cleavage, is determined, partially at least, by the same factors which determine the form and relative position of soap bubbles in a mass. As a result of surface tension, the cells take such forms as to occupy the given space with the least possible surface areas. New septa will appear in such positions that their surfaces will be the least possible areas that could divide the cell into parts of the required size. "Die Lamellensysteme ordnen sich so an, die einzelnen Lamellen krümmen sich in der Weise, dass die Summe der Oberflächen aller unter den gegeben Verhältnissen ein Minimum wird." (Berthold, '86, pp. 219, 220.)

(2) *Hertwig's law of the spindle in the longest axis of the protoplasmic mass.* — According to Hertwig's well known view, as a result of the interaction of nucleus and protoplasm, the spindle during division comes to lie in such a position that its longitudinal axis coincides with the axis which passes through the greatest protoplasmic mass. "Es lässt sich hier das zweite allgemeine Gesetz aufstellen, dass die beiden Pole der Theilungsfigur in die Richtung der grössten Protoplasmamassen zu liegen kommen, etwa in derselben Weise, wie die Lage der Pole eines Magneten durch Eisentheile in seiner Umgebung beeinflusst wird." (Hertwig, '93, p. 175.)

(3) *Braem's theory of separation in the direction of the greatest space for development.* — This is a modification of the principle of least pressure, first enunciated by Pflüger ('84). Since Pflüger's principle, considered from a purely mechanical standpoint, seems irreconcilable with the nature of the material on which it was supposed to act, and since Braem's view is based on an essentially different conception of the nature of the phenomena, I have not thought it necessary to take into direct consideration Pflüger's view.

Braem holds that when an egg is subjected to unequal pressure, the spindle places itself in such a position that the resulting products shall have the freest opportunity for development; that is, in the direction of least resistance. The rule is not the expression of a purely mechanical force, but is to a certain extent teleological in character. "Die Spindel eines ungleichem Druck unterliegenden Eies stellt sich in derjenigen Richtung ein, in welcher der räumlichen Entfaltung der Zelle und ihrer Teilprodukte der freieste Spielraum geboten ist. Ich glaube, dass diese Fassung trotz oder vielmehr gerade wegen ihres teleologischen Gehaltes dem Wesen der Sache besser entspricht als die rein mechanische Deutung." (Braem, '94, pp. 341, 342.)

The result is held to be due to a sort of sensory power resident in the egg, "eine Art Tastsinn, durch den es der Zelle möglich wird, sich aber ihre unmittelbare Umgebung zu orientieren und demgemäss einzurichten." (p. 342.)

(4) *Roux's theory of a compromise between the tendency immanent in the nucleus and the tendency due to the form of the protoplasmic mass.* — Roux holds that the spindle places itself in one of the positions of stable equilibrium in relation to the protoplasmic mass, — therefore, at least generally, in the longest axis of the protoplasmic mass, though sometimes at right angles to that axis, the factor that decides which of these positions shall be taken being an immanent tendency in the nucleus to divide in a certain direction.

"Richtiger ist es zu sagen: Die Kernspindel der Furchungszellen stellt sich in die, resp. in eine Richtung festesten Gleichgewichtes der tractiven Einzelwirkungen der Protoplasmamasse. Diese Richtung entspricht überwiegend häufig annähernd oder ganz der grössten durch den Mittelpunkt der Protoplasmamasse gehenden Dimension.

"Diese Richtung des Gleichgewichtes wird aber nicht vollkommen vom Protoplasma allein bestimmt, sondern sie kann, wie ich bereits 1884 und 1885 auf Grund von Experimenten erschlossen habe, von der Lage der immanenten Teilungsrichtung des Kernes zu den Hauptrichtungen des Protoplasmakörpers abhängig sein; denn ich erhielt bei symmetrisch gestalteten 'linsenförmig' deformirten, mit den grössten Fläche senkrecht stehenden Froscheiern *zwei* Prädictionsrichtungen der Spindeleinstellung: die Richtung der grössten und der kleinsten durch den Massenmittelpunkt gehenden Dimension, erstere allerdings wieder die überwiegend häufige." (Roux, '94, p. 152.)

It is to be noted that this theory does not attempt to give any rule by which the position of the spindle is necessarily determined; the tendency of the nucleus is simply "immanent," and its factors unknown.

In addition to these four well characterized theories, a number of less definite or partial views have been set forth, — some proposing factors which may influence, though not alone determine, the position of the spindle. A number of the more important of these will be mentioned.

(5) *Heidenhain's problem of a definite angle of rotation* ("Problem der gesetzmässigen Drehungswinkel"). — Heidenhain ('94, p. 719) thinks it probable, or at least possible, that careful investigation will show that in a given tissue the position which the spindle takes at the time of division is a result of its rotation through a definite angle, determinable for the given tissue, after the first formation of the spindle by the separation of the asters. This separation of the asters is held

to be at first in a line at right angles to the axis of the preceding spindle; then, by a rotation through an angle characteristic for the tissue, the definitive position is reached. The position which the spindle is finally to take is therefore determined at the time the asters separate. "Soweit ich indessen die Lage übersehen kann, ist die schliessliche Stellung der Spindel von dem Moment an fest gegeben, in welchem die Theilung des Muttermikrocentrums stattfand." (Heidenhain, '95, pp. 555, 556.)

(6) *Sachs's view, that the walls separating the cells meet one another at right angles.* — This (Sachs, '78, p. 1070) can hardly be considered as more than a statement of a condition commonly found. Berthold ('86, p. 252) and Hertwig ('93, p. 177) have endeavored to show that the condition is explainable as a result of the theories proposed by them.

(7) *Rauber* ('83, p. 276) *holds that there is evidence that the asters of the different blastomeres exercise an attraction for each other in such a way that, in a given area composed of a number of cells, the spindles must take such positions as to bring about a condition of equilibrium among the asters.* — "Beurtheilt man die Verschiedenheiten der Furchennetzes von der Stellungen der karyokinetischen Achsen aus, so gewinnt es den Anschein, als ob die neu entstehenden Centren eines Blastomers auf diejenigen der angrenzenden Blastomeren einzuwirken vermögen und die Richtung ihrer Achsen beeinflussen." (Rauber, '83, p. 280.)

(8) *Braem's principle of equal resistance at the two ends of the spindle.* — Subordinate to his principle of least resistance, Braem holds that the spindle tends to take such a position that the pressure at the two ends is the same. "Es ist das Princip des *gleichen* Widerstandes, wodurch die horizontale Lage der Spindel bedingt wird. Wir müssen annehmen, dass der Kern von vornherein das Bestreben hat, sich gleichmässig nach beiden Seiten hin auszudehnen und somit auf eine äquale Zellteilung hinzuwirken." (Braem, '94, p. 345.)

In the following description these theories will be kept in mind, and the bearing of the observations upon them pointed out. It will appear that, for certain of the theories, the conditions in the egg of Asplanchna present crucial tests.

B. *Equality or Inequality of Cleavage.*

The second aspect under which cleavage is determined is with regard to the *relative size* of the two products. What is it that determines whether the division shall be equal or unequal?

Concerning the factors which determine the equality or inequality of cleavage, two theories have been proposed. According to the view which is perhaps that most generally known, the cause of unequal cleavage lies in the relative distribution of yolk material and formative protoplasm. The interaction between nucleus and cell contents, which determines the position of the dividing nucleus, exists only between the nucleus and the formative protoplasm, not between the nucleus and the yolk material. As a consequence of this interaction, the nucleus tends to take a position in the centre of the mass of *formative protoplasm*. When one region of the cell is composed largely of yolk material, in a mere meshwork of protoplasm, while another region is made up entirely of protoplasm, the dividing nucleus must separate equal masses of formative protoplasm, and thus may divide the *entire* mass into very unequal parts, — one containing a certain mass of protoplasm only, the other an equal mass of protoplasm and a large additional mass of yolk material. The theory has recently been formulated by Hertwig as follows: "Die Folge dieser Wechselwirkung aber ist, dass der Kern stets die Mitte seiner Wirkungssphäre einzunehmen sucht. . . . Wechselwirkungen finden zwischen dem Kern und dem Protoplasma, nicht aber zwischen ihm und dem Dottermaterial statt, welches bei allen Theilungsprocessen sich wie eine passive Masse verhält. Ungleichmässigkeiten in den Protoplasmavertheilung müssen sich daher auch auf Grund des obigen Satzes in der Lage des Kerns geltend machen, und zwar muss derselbe nach den Orten der grösseren Protoplasmaansammlung hinrücken." (Hertwig, '93, pp. 172 and 174.)

Braem's principle of equal resistance at both ends of the spindle is in character related to this view of Hertwig. Besides the effect of it in determining the direction of the spindle, this supposed principle is likewise of effect in determining the equality or inequality of cleavage, as appears from the quotation from Braem given on page 7.

C. *Determination of the Time of Division, or the Interval between Successive Cleavages.*

The same factor which is held to determine the relative size of the cells was also held by Balfour, with whom Hertwig agrees (Hertwig, '93, p. 180), to determine the relative rapidity of cleavage. The greatest interval between successive cleavages is found in cells which contain the greatest amount of yolk relative to the amount of contained protoplasm. "The rapidity with which any part of an ovum segments varies *ceteris paribus* with the relative amount of protoplasm it contains; and the size of the segments formed varies inversely to the relative amount of the protoplasm." (Balfour, '80, p. 99.)

D. *Differentiation during Cleavage.*

Besides these questions in regard to the form and rate of cleavage, we have also the question of the *qualitative nature of cleavage.* Is cleavage merely a quantitative process, or is it accompanied by a differentiation of the separated cells? And if the latter is the case, by what means is this differentiation accomplished?

The view once maintained, that cleavage is entirely unaccompanied by differentiation of the separated cells, may be said to be nearly or entirely given up; the questions which remain relate to the means by which this differentiation is brought about. In regard to this several well defined views exist.

1. Roux holds that the differentiation accompanying cleavage is a result of qualitative karyokinesis; i. e. at a given cell division the two products receive *nuclear* material of different nature.

2. Driesch maintains that the differentiation which may accompany cleavage is due to the specific *cytoplasmic* structure of the egg, different parts of the egg being of different constitution, so that when this differentiated mass is separated into parts, these parts receive different sorts of cytoplasm. That is, the qualitative division is in the cytoplasm, not in the nuclear material. "Ich habe schon oben gesagt, dass ich ein Verschiedenwerden der Furchungszellen während der Furchung gern zugebe, aber hierin nichts anderes als die Folge eines spezifischen Plasmabaus des Eies sehe." (Driesch, '94, p. 100.)

3. According to Wilson and Hertwig the differentiation accompanying cleavage is due, largely at least, to the interaction of the blastomeres, after division has taken place. This does not exclude the possibility of the existence at the same time of a qualitative division of the cytoplasm, as stated above (2).

2. Later Developmental Processes.

With regard to the later developmental processes, it will not be necessary to give here a review of the various factors and theories which have been set forth by different authors. Driesch ('94) gives an extended analysis of the morphogenetic process and its factors, and Davenport ('95) presents a detailed list of the different processes concerned in development. It is sufficient here to propose a single question: What is the relation of the cleavage process to the secondary morphogenetic processes? Driesch's well known experiments indicate that, in the case of the sea-urchin, the manner of cleavage is entirely unimportant for the later morphogenetic processes. Gastrulation, for example, occurs in the same manner, after the most varied and fundamental alterations of the cleavage. Is this a fact which is capable of generalization, — of application to different animals and different methods of gastrulation? Doubtless the only positive answer to this question must come from experimental studies; but a careful descriptive analysis of the process in Asplanchna gives results which, if the egg were a mechanism of the ordinary physical sort, would be definite and conclusive.

II. Descriptive Portion.

1. Form and Structure of the Egg.

The development of the embryo in Asplanchna Herrickii takes place within the body of the mother, the egg lying enclosed in the enlarged oviduct, close to the ovary. The chief axis of the developing embryo bears no relation to the position of surrounding organs of the mother, the egg lying in the oviduct as it might within a protecting sac of any foreign material, its position determined by chance circumstances. In cases where two embryos are present, their axes may make any angle with each other.

For study it is necessary to dissect out the eggs. A full account of the methods of work is given in Part Third; here it is important to note two facts: (1) All the work was done on preserved material; (2) Each egg comes from a different individual, and is therefore in at least a slightly different stage from every other. A considerable number of eggs showing any given process, as, for example, the first cleavage, gives therefore a series of stages, so that a complete idea of the changes taking place may be gained.

The unsegmented egg is approximately an ellipsoid of nearly equal axes, one end often slightly more pointed than the other. The form and proportions vary a little, as do also the absolute dimensions. In many eggs it is difficult to distinguish a more pointed end. The proportion of the longer to the shorter axis is about as 9 to 8, and the average dimensions of the egg are about $90\,\mu$ through the longer axis by $80\,\mu$ through the shorter. Variations from a minimum of $84\,\mu$ by $70\,\mu$ to a maximum of $97\,\mu$ by $83\,\mu$ were observed.

Whether an egg membrane is present or not is exceedingly difficult to decide; and I have not succeeded in thoroughly satisfying myself upon that point. The walls of the oviduct invest the egg closely, and generally cannot be removed, so that a thin membrane, if present, could not be detected. In most cases where it was possible to remove the walls of the oviduct entirely, no membrane could be seen either in sections or whole preparations, the egg appearing to be naked. In a few cases, however, in which cleavage had recently taken place and the cleavage furrows were marked, it could be observed that the smooth outline of the egg was preserved even above the cleavage furrow, either by means of a membrane continuing across the furrow, or, what seemed from the appearance of the preparations more probable, owing to the presence in the furrows of a fluid mass, perhaps exuded from the egg. Such a case is shown in Plate **1**, Fig. 4. On other grounds, however, it seems possible that an extremely delicate membrane is present. Lameere ('90) states that in Asplanchna Sieboldii, which is likewise viviparous, it was possible to observe definitely a very delicate membrane surrounding the egg, especially at the time of the formation of the polar cell.

This question of the presence or absence of an egg membrane is of importance from a mechanical standpoint, owing to its bearing upon the question as to what preserves the ellipsoidal form of the egg. The form is retained throughout all the early developmental processes; cleaving cells do not project above the general surface of the egg, nor do the products of cleavage become spherical, touching at a few points only, as is common in the Mollusca and other groups. This retention of the ellipsoidal shape by the egg compels the cleaving cells to take various peculiar forms, which allow of a direct test of some of the theories of cell division above stated. It is also a most important factor in the process of gastrulation, so that it becomes of great interest to discover what it is that preserves this form.

It is evident that surface tension would tend to produce a spherical rather than an ellipsoidal form. Roux ('95) has recently proved that blastomeres have a direct attraction for each other; but an equal attraction throughout the mass would produce a spherical form, and an unequal attraction, such as would produce a regularly ellipsoidal form, is very difficult to conceive of, especially as this attraction would have to vary regularly with the shifting of the contents of the egg. A membrane of equal elasticity in all parts would likewise result in the production of a spherical form. The only direct mechanical factor that seems capable of explaining the continued ellipsoidal form is the presence of a non-elastic membrane of the exact size and shape of the egg. But during the later development the embryo enlarges and changes its form;

the membrane cannot therefore be absolutely inelastic, but might be of such strength as to act as an inelastic membrane with regard to such slight forces as are exerted within the egg during its early development. The existence of a membrane of this peculiar character is, however, very improbable, and it loses all its explaining power when the egg of another rotifer, Melicerta ringens, is taken into consideration. In this species the egg is not a regular ellipsoid or oval, but is of an irregular shape, one side being curved in profile, the other straight. (See the figures of Zelinka, '91.) This form is retained during development exactly as in Asplanchna, yet is not explainable on the assumption of a membrane. This question is discussed more fully later.

The cytoplasm of the egg is closely filled with fine yolk granules. These are distributed uniformly throughout the egg (except that they are not present in the asters), so that there is no visible differentiation into regions containing greater and less amounts of yolk material.

The development of Asplanchna priodonta Gosse was also examined for comparison with that of Asplanchna Herrickii. The egg of this species is similar throughout to that of Asplanchna Herrickii, save that it is smaller. The average dimensions are about 70 μ by 60 μ. The egg of Asplanchna priodonta is shown in Figure 29, Plate **4**, drawn to the same scale as the figures from Asplanchna Herrickii.

2. Maturation.

The formation of the polar cell in Asplanchna Sieboldii has been described by Lameere ('90) from observations upon the living egg. The general features of the process are similar in Asplanchna Herrickii, though the finer nuclear phenomena differ from those described by Lameere. An account of the finer nuclear phenomena is, however, foreign to the purpose of this paper: it is necessary to describe merely the general features of the process, especially concerning the place where the process occurs, in relation to the later orientation of the embryo.

As is now well known, but a single polar cell is commonly formed in the parthenogenetically developing eggs of the Rotifera. The subject has received full discussion, especially by Weismann und Ischikawa ('87) and Lameere ('90). It may be noted that Zelinka ('91) observed that in a number of eggs of Callidina two polar cells were formed; whether these arose by division of a single one, or whether the two were formed separately from the egg, is not stated. In no case have I obtained any evidence indicating the formation of more than a single polar cell in Asplanchna.

In immature eggs the large germinative vesicle is commonly found in an eccentric position, with no very apparent relation to the axes of the egg. In Asplanchna Sieboldii, according to Lameere ('90), just before the movement of the germinative vesicle toward the spot where the polar cell is formed, it lies in the long axis of the egg nearer one pole, — in the position where later the first cleavage spindle is located. This is probably the case also in Asplanchna Herrickii; but before the germinative vesicle has begun to show the changes indicating the formation of the maturation spindle it is difficult in preserved material to get evidence as to the proper sequence of the stages observed.

Just before the maturation spindle is formed, the nucleus moves toward the periphery of the egg, and begins to lose its spherical shape. It takes a position close to the surface, not at the equator, but nearer one of the poles of the egg, as shown in Figure 1. In cases where the differentiation into a more pointed pole and a blunter one is visible, the nucleus always lies nearer the more pointed pole. Here a spindle is formed, and the maturation division takes place. The polar cell thus formed does not lie upon the outer surface of the egg as a free body, but from the first is pressed into the substance of the yolk (Fig. 2), as if by a firm membrane, in the manner described by Lameere for Asplanchna Sieboldii. The nucleus begins to withdraw from the periphery, at the same time resuming the spherical form, leaving the polar cell a flattened, disk-like body, not projecting above the general surface of the egg. This condition of the egg is shown in Figure 2.

From the first, therefore, the polar cell is imbedded in the substance of the egg, so that it cannot suffer displacement during the processes which follow. As will be shown in the course of this paper, the place where the polar cell is formed marks the point on the surface of the egg opposite to that at which gastrulation takes place. This is contrary to the statement made by Zelinka ('91) for the egg of Callidina, and contrary to his general statement for the Rotifera as to the relation of the place of polar cell formation to the later axes of the embryo. As this matter is not of especial interest from the standpoint of developmental mechanics, a full discussion of the difference between my account and that of Zelinka is reserved for Part Second. There it will be shown by evidence from Zelinka's own work, as well as that presented here, that his general statement of the relation of the place where the polar cell is formed to the axes of the egg in the Rotifera cannot be considered true for other forms than Callidina russeola, whatever may be the conditions in that species.

3. Orientation of the Developing Embryo.

The first cleavage plane is transverse to the long axis of the egg, and divides it into two unequal parts (Figure 6). The plane passes through the place where the polar cell was formed; the smaller cell includes, therefore, that end of the egg nearest to which the polar cell is located. As previously stated, this is also the more pointed end of the egg, when any difference in the two ends is distinguishable.

The second cleavage is approximately at right angles to the first, and nearly in the long axis of the egg. It also passes through the region where the polar cell was formed.

As previously stated, the oval or ellipsoidal form of the egg is retained throughout the early development. This form is independent of the precise arrangement of the material of which the egg is composed. It is as if the egg substance were enclosed in a rigid mould of oval or ellipsoidal form. Within this mould the (fluid?) contents may shift their position widely, without influencing the form of the mould. Thus, at the first cleavage, the material of the smaller blastomere occupies all of one end of the egg. In the ten-cell stage (Plate **3**, Figs. 20–25) the same *form* is still preserved as if in a rigid cast, but the *material* which previously formed the smaller of the first two blastomeres has shifted from the end to one side of the egg. It therefore is necessary to have some term by which to designate the two ends of this constant *form*, as distinguished from the shifting blastomeres themselves. I shall henceforth speak of that end of the egg at which lies the smaller cell in the two-cell stage as the *micromere* end of the egg, while the opposite region, where the larger blastomere lies, will be called the *macromere* end. These terms refer to the *form* of the egg, without regard to the shifting contents.

The orientation which I shall adopt for the egg itself is similar to that used by Wilson, Heymons, Conklin, Lillie, Kofoid, and other recent workers on cell lineage. The region where the polar cell is formed, and which afterward lies opposite the blastopore, will be called the *animal pole*: it marks the *dorsal surface*. The opposite point is the *vegetative pole*, marking the *ventral surface*, — the position of the future blastopore. *Dorsad* signifies always toward the animal pole, or place where the polar cell was formed; *ventrad*, in the opposite direction, toward the region where the blastopore is found at a late stage. The orientation is thus based upon the structure of the *gastrula*. The *chief axis* of the gastrula is the line connecting the animal and vegetative poles.

The first cleavage plane, though coinciding with the chief axis of the *gastrula*, is, as shown by the later development, transverse to the long axis of the *embryo*. The smaller cell of the two-cell stage is *anterior*, since its products occupy the anterior margin of the blastopore; the larger cell is *posterior*, its products forming the posterior lip of the blastopore. The second cleavage plane, though modified in the posterior part of the egg, is approximately longitudinal. In the four-cell stage (Plate **2**, Fig. 8) the two cells A^3 and B^3, resulting from the division of the smaller cell, $\overline{AB}^2$, are respectively left anterior and right anterior, while C^3 and D^3, produced by the division of the larger cell, $\overline{CD}^2$, are respectively right and left posterior.

A section taken transversely to the chief axis of the gastrula will be spoken of as a *transverse section*. A section at right angles to this, passing from anterior to posterior and including the animal and vegetative poles, is a *sagittal* section. A section at right angles to both of these, cutting both the animal and the vegetative pole and passing through the right and left sides, is a *frontal* section.

As will be seen from the above, in the two-cell and four-cell stages, the micromere end coincides with the anterior, the macromere end with the posterior end.[1]

The orientation given above is based upon the relation of the egg to the axes of the gastrula; the same is true of the orientation used in most of the recent works upon cell lineage. It differs fundamentally from the orientation used by Zelinka ('91) for the developing egg of the rotifer Callidina russeola. In that species the egg is of the same form as in Asplanchna. After extensive shifting during development, the anterior end (in both Asplanchna and Callidina) comes to lie in the region of that end of the egg which I have called the macromere end. Zelinka calls this end of the egg, therefore, the anterior end, the opposite (my micromere end) the posterior end. Anterior and posterior in Zelinka's orientation of course remain constant with regard to the *form of the egg*, but not with relation to the *parts of the embryo*. Thus, if

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[1] It is of the greatest importance to observe that I do not use the terms "micromere end" and "macromere end" in the same sense in which "micromere pole" and "macromere pole" are sometimes used, as synonymous with "animal pole" and "vegetative pole." The two terms are used only as a convenient way of indicating a *peculiarity* of the rotifer egg.

Zelinka's orientation were adopted, the point where the polar cell is formed might be first ventral, then posterior, then dorsal, and later anterior, and this would actually be the case in Asplanchna. In a special study of cleavage, with particular attention to direction, it is necessary that the orientation should give some *constant* basis for reference. It is therefore impossible for me to use Zelinka's orientation in my work. The animal pole of the egg *does* retain, however, a constant relation to the position of the blastomeres and to the axes of cleavage, so that I have adopted this relation as a basis for orientation.

4. Cleavage.

Nomenclature.

For accurate comparative study of the direction and sequence of cleavage in the different regions of the egg, such a system of nomenclature is needed as will indicate directly the relationships, and especially the comparative age (measured in cell generations) of the blastomeres. The only system of nomenclature hitherto proposed which fulfils these demands is, I believe, that of Kofoid ('94). I shall therefore use his system in the following account.

The four blastomeres of the four-cell stage, and the cells derived from them, are designated respectively by the letters *A*, *B*, *C*, and *D*, beginning with the left anterior blastomere and passing around the egg to the right, i. e. in the same direction as the hands of a watch, — assuming the egg to be viewed from the animal pole. The letters thus represent the same blastomeres as in Wilson's work ('92) on Nereis, Heymons's ('93) on Umbrella, Lillie's ('95) on Unio, and Kofoid's ('95) on Limax.

After the first equatorial cleavage, at which the four original blastomeres are divided into smaller cells, the capital letters *A*, *B*, *C*, and *D* will be reserved to indicate respectively *all* the cells derived from the corresponding cell of the first four blastomeres; and such a collection will be called a *quadrant* of the egg.[1] The separate cells will be designated by the lower-case letters *a*, *b*, *c*, and *d*, according to the quadrant to which they belong. Each letter will be followed by two exponents. The first exponent indicates the generation to which the cell belongs, the unsegmented egg being considered the first generation. Thus, in the eight-cell stage (fourth generation) we shall have cells a^4, b^4, c^4, and d^4. Since, however, in this and in later generations, there are more than one cell of a given quadrant in a given generation, this first exponent must be followed by a second, serving to distinguish each cell from every other of the same quadrant. In "spiral" cleavage, this second exponent indicates the "quartet," or layer of cells, in the embryo to which the blastomere belongs, the *ventral* cell being number 1, the next dorsal number 2, and so to the most dorsal quartet. In equatorial cleavages the same relation may be preserved in other types of cleavage than the spiral. Thus, in the eight-cell stage (fourth generation), the ventral blastomeres are $a^{4.1}$, $b^{4.1}$, $c^{4.1}$, and $d^{4.1}$, while the corresponding dorsal cells are $a^{4.2}$, $b^{4.2}$, $c^{4.2}$, and $d^{4.2}$. But in meridional cleavages, where there is no trace of the so called spiral, this criterion fails, and the second exponent can be used only for distinguishing the cells, not for indicating their relative positions. What is required is a rational system of applying the exponent such that no two cells of the same quadrant in the same generation shall have the same exponent. Following the suggestion of Kofoid ('94), I have in meridional cleavages designated the *right* derivative with the *even* exponent in *even* generations, and with the odd exponent in odd generations, — the left derivative of course receiving the reverse designation. This method of application was designed to preserve any possible homologies of the products of meridional with those of spiral cleavage, since in normal spiral cleavage the right derivative lies above the left in even generations, and so receives the even exponent, while in odd generations the reverse is true. The results, however, have not shown any striking homologies with spiral cleavage, but the method of application has been retained, since no other seems to have any advantage over it.

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[1] Each quadrant from the four-cell stage onward receives a specific color in the plates, so that the quadrants are instantly distinguishable by their colors.

In meridional cleavages, the terms *right* and *left* will be used as defined by Kofoid ('94, p. 180): "A miniature observer is imagined as placed in the principal (vertical) axis of the egg, with his head at the animal pole, facing the part or parts under consideration, and the terms *right* and *left*, *upper* and *lower*, are used as determined by this observer."

A full account of this system of nomenclature is given by Kofoid ('94). In order to make clear the relation of the succeeding blastomeres and their designations by this system, I give here a scheme of the nomenclature through the sixth generation, modified from that given by Kofoid. Only the products of quadrant *A* are carried out beyond the third generation, since the method is the same for the other quadrants. Here $a^{6.1}$ represents the most ventral cell derived from the blastomere A, while $a^{6 \cdot 8}$ represents the most dorsal one, the others occupying intermediate positions.

				$a^{5 \cdot 4}$	$a^{6 \cdot 8}$
			$a^{4 \cdot 2}$		$a^{6 \cdot 7}$
				$a^{5 \cdot 3}$	$a^{6 \cdot 6}$
					$a^{6 \cdot 5}$
		A^3			
	$\overline{AB}^2$			$a^{5 \cdot 2}$	$a^{6 \cdot 4}$
			$a^{4 \cdot 1}$		$a^{6 \cdot 3}$
		B^3			$a^{6 \cdot 2}$
$\overline{ABCD}^1$		C^3		$a^{5 \cdot 1}$	$a^{6 \cdot 1}$
	$\overline{CD}^2$				
		D^3			
1 cell.	2 cells.	4 cells.	8 cells.	16 cells.	32 cells.

First Cleavage.

After the formation of the polar cell the nucleus (Plate **1**, Fig. 2) returns to the position formerly occupied by the germinal vesicle in the longitudinal axis of the egg, lying nearer that end of the ovum in proximity to which the polar cell was formed (the micromere end). It takes such a position that a plane at right angles to the long axis of the egg and cutting the polar cell would also cut the nucleus. The distance from the centre of the nucleus to the nearer end of the egg is about two fifths of the length of the egg. Here two asters appear on opposite sides of the nucleus, the line joining them being oblique to the long axis of the egg. Though I have examined a large number of eggs at this stage, in no case have I been able to observe a stage in the process of forming the two asters of the first cleavage spindle (Fig. 3) from the single aster remaining after the formation of the polar cell (Fig. 2).

Between the two asters a spindle is formed. This lies at first somewhat oblique to the longitudinal axis of the egg, as shown in Figure 3, but before cleavage takes place the spindle swings into coincidence with the long axis (Fig. 4). The aster lying at the micromere end of the spindle is distinctly smaller than the opposite one (Fig. 3). The nucleus becomes divided into two small masses, which move toward opposite ends of the egg, but remain connected for a time by a distinct strand (Fig. 4). Meantime, before the first cleavage plane has appeared in the cytoplasm, the aster of the smaller blastomere has begun to divide, as shown in Figure 4. The two resulting asters separate at right angles to the axis of the first cleavage spindle. In the future larger cell the aster does not begin at once to divide. Both nuclei begin immediately to increase in size. The first cleavage plane passes through the point on the surface of the egg marked by the polar cell, transversely to the long axis of the ovum, and through about the middle of the strand connecting the two nuclei. The strand is slightly thickened at the point where the first cleavage plane is to meet it (Fig. 4), indicating perhaps the formation of the "Zwischenkörper." The cleavage plane is thus perpendicular to the axis of the spindle, and passes through its middle. I mention this fact on account of the difference between the first cleavage of Asplanchna and that of Callidina. In the latter rotifer, according to Zelinka ('91), the first cleavage plane is oblique to the spindle, and the spindle itself, even at the time of division, is oblique to the long axis of the egg. In another rotifer, Eosphora, the first cleavage plane is likewise oblique to the long axis of the egg (Tessin, '86), while in Melicerta ringens (Zelinka, '91) and Asplanchna Sieboldii (Lameere, '90) the first cleavage plane is transverse to the long axis, as in Asplanchna Herrickii.

During and after the passage of the first cleavage plane through the cytoplasm, the egg retains its ellipsoidal form, and the resulting cells do not separate and become rounded, as occurs in the eggs of so many animals, but remain closely pressed together. In a large series of cases showing the first cleavage in various stages, the only indication of any change in the form of the egg or its blastomeres is a slight depression of the surface where the cleavage plane cuts the periphery of the egg, forming a shallow furrow. Here the edges of the two blastomeres are slightly rounded off, as shown in Figure 6, instead of fitting squarely against each other. The retention of its general form by the egg is characteristic of all cleavage stages. This surface of contact of the two blastomeres is curved, the smaller cell, $\overline{AB}^2$, projecting slightly into the larger.

So far as the direction of the division is concerned, the first cleavage of Asplanchna evidently fits easily either the surface tension theory of Berthold, or Hertwig's theory of the spindle in the long axis of the protoplasmic mass. Comparison with the first division of Callidina russeola as described by Zelinka ('91) develops an interesting fact. In

Callidina the first cleavage spindle is *oblique* to the long axis of the egg, therefore not in agreement with Hertwig's law; but immediately after division is finished, a movement of the egg contents takes place in such a way that the two cells occupy the same relative position as in Asplanchna, — such a position, therefore, as is demanded by Berthold's theory of least surfaces. It thus appears that in Callidina the direction of division itself is determined neither by the principle of Berthold nor that of Hertwig, but that the later arrangement of the cells might be held to be due to the action of Berthold's principle. It is somewhat curious that the exact arrangement produced in Callidina by shifting should in Asplanchna result at once from the position of the spindle at the time of cleavage.

No cause can be assigned, from the visible structure of the egg, for the inequality of the cleavage. The yolk granules are distributed uniformly throughout the egg, seeming no more abundant in the large than in the small cell.

Second Cleavage.

As a result of the first cleavage, the egg is now composed of two unequal blastomeres, an anterior, $\overline{AB}^2$, and a posterior, $\overline{CD}^2$ (Figs. 5 and 6).

In the smaller blastomere, as previously stated, the aster has already divided and the two parts are separating at the time when the first cleavage plane passes through the cytoplasm (Fig. 4). The line along which they move apart is perpendicular to the axis of the first cleavage spindle, and also at right angles to a line connecting the polar cell with the centre of the egg. The forming spindle is thus parallel to the lateral axis of the embryo and consequently perpendicular to its dorso-ventral axis. The two asters take up their positions on opposite sides of the nucleus, and the axis of the resulting spindle has a direction parallel to the line joining the asters at their first separation (Figs. 5 and 6). Meanwhile the nucleus has steadily increased in size, up to the time when it participates in the formation of the spindle.

In the larger cell, $\overline{CD}^2$, the order of procedure is different. The nucleus begins to enlarge, as in the smaller blastomere, but the aster does not at once divide. The nucleus and aster together begin to migrate to the right. At the same time the aster comes to lie farther to the right than the nucleus, either because the two rotate on a common axis, or because the aster, moving faster, creeps around the nucleus toward the right side of it. Thus, whatever the method, a condition is reached in which the large nucleus lies in the right anterior angle of the cell $\overline{CD}^2$, with the undivided aster at its right and slightly behind it (Fig. 5).

By this time the two asters in the cell $\overline{AB}^2$ have completely separated and lie upon opposite sides of the enlarged nucleus. Thus the preparatory stages for karyokinesis are much more advanced in the smaller cell, and it would be anticipated that this cell would cleave first.

The single aster in $\overline{CD}^2$ now begins to divide. The process seems to be accomplished very quickly, since in a series of nineteen specimens of the two-cell stage (each, of course, taken from a different individual) only one case was found exhibiting a transitional stage between that shown in Figure 5 and that shown in Figure 6. In this specimen the single aster had elongated slightly in the direction of the future spindle. When formed, the spindle takes an oblique position in the cell, extending from right anterior to left posterior. The aster at the left posterior end of the spindle is much the larger, in correlation apparently with the larger mass of cytoplasm surrounding it. The nucleus of $\overline{CD}^2$ has now overtaken in its metamorphosis that of $\overline{AB}^2$; the spindles are found in exactly corresponding stages, the chromatin being in both arranged in an equatorial plate (Fig. 6).

Not only are the two spindles not parallel, as shown in Figure 6, but they do not lie in the same plane. If the two spindles are viewed exactly from the anterior or from the posterior end of the egg, the left aster in $\overline{AB}^2$ and the right aster in $\overline{CD}^2$ are seen to lie more dorsally than their mates. Viewed in this direction, the spindles cross each other at an angle of about twenty-five degrees.

As a result of the dissimilarity in the direction of the two spindles, the two next cleavage planes, perpendicular to them, will not meet the first cleavage plane in a common line. The position and direction of the spindle in $\overline{CD}^2$ are such that the cleavage plane cutting $\overline{CD}^2$ would probably meet the first cleavage plane to the right of the line where the plane dividing $\overline{AB}^2$ would meet it. Since the right aster of $\overline{CD}^2$ is farther dorsal than the left, the plane of cleavage of CD^2 would be inclined to the sagittal plane, — on the dorsal side toward the left, on the ventral side toward the right.

The cleavage of the two cells now follows at almost or precisely the same time, the karyokinetic processes being found from this time on in the same stage. In a series of thirty-one eggs from different individuals, each containing more than one and less than five cells, none contained exactly three cells.

An examination of the four-cell stage after the completion of division

(Plate **2**, Fig. 8) shows that the cleavage planes have taken the positions foreshadowed by the arrangement of the spindles. The plane separating C^3 from D^3 lies to the right of the plane separating A^3 from B^3; the corresponding furrows on the surface are nearer together on the dorsal than on the ventral side. The blastomeres resulting from the division of $\overline{AB}^2$ are equal, whereas $\overline{CD}^2$ divides very unequally. The right derivative (C^3) is much smaller than the left (D^3), and is of approximately the same size as A^3 and B^3. The blastomeres B^3 and D^3 are in contact along the whole distance from the dorsal to the ventral surface of the egg, while A^3 and C^3 do not touch each other at all. The polar cell lies either at the junction of B^3, C^3, and D^3, as shown in Figure 8, or sometimes at the junction of A^3, B^3, and D^3. The egg is now markedly unsymmetrical.

It is evident from the above description that this cleavage may be considered as belonging to the so called spiral type. Since the left end of the spindle is in each cell the higher, the cleavage is a left spiral, like the corresponding cleavage in Discocelis, Nereis, Limax, and indeed all forms with spiral cleavage except in the reversed cleavage of certain mollusks. This fact is striking, since the succeeding cleavages in Asplanchna *do not belong to the spiral type.*

The relation between the axes of the embryo in later stages and the first two cleavage planes is as follows. The first furrow separates an anterior from a larger posterior portion, but the plane of separation of the parts bears no simple relation to the axes of the later embryo. (Compare Figure 8 with Figure 75, Plate **9**, in which the parts derived from the first four cells are colored in the same manner as their parent cells in Figure 8, and note the great shifting.) The later sagittal plane of the embryo is coincident with a plane passing through the animal pole and the longest axis of the egg; that is, through the plane separating A^3 from B^3 (Fig. 8), and dividing the larger blastomere D^3 into two unequal parts. The second cleavage plane therefore divides the right side from the left in the anterior part of the egg; but in the posterior part it lies entirely in the right side. It is not until the seventh cleavage that the division into symmetrical right and left halves takes place on the posterior side (Plate **7**, Fig. 58); indeed, certain cells containing material for both sides of the egg remain undivided till even a later stage.

Third Cleavage.

Immediately after the second cleavage, the aster in each of the four cells produced begins to extend dorso-ventrally, at right angles to the axis of the preceding spindle. An optical section of the egg along its chief axis, showing the asters in the cells B^3 and D^3, is given in Plate **2**, Fig. 10. Spindles are formed in all four cells nearly or quite in the position indicated by the direction of separation of the asters.

The tendency of the karyokinetic processes in the posterior half of the egg to gain upon those in the anterior half, shown during the last division, is continued and accelerated. Spindles appear in C^3 and D^3, while the nuclei in A^3 and B^3 are still spherical and have distinct membranes. Figure 9 gives a view of this stage from the right side; the large spherical nucleus of B^3 is represented by a broken outline. The spindle in C^3 has a dorso-ventral direction, and its middle coincides with the middle of the length of the cell; the two asters are of equal size. In D^3 the spindle is nearer the dorsal side of the egg, and is inclined, passing from dorsal and anterior to ventral and posterior. The ventral aster is the larger.

Cleavage takes place first in the larger cell D^3, separating a large ventral blastomere, $d^{4.1}$, from a smaller dorsal one, $d^{4.2}$. At the same time the two cells (considered as a whole) elongate dorso-ventrally. In so doing, the ventral blastomere, $d^{4.1}$, remains nearly stationary, while $d^{4.2}$ moves in the direction of the animal pole of the egg. (Compare Figure 12, a sagittal section of a five-cell stage, with Figure 10, the corresponding section of a four-cell stage, observing the position of the cells in relation to the general form of the egg.) As a result of this, the dorsal end of the cell B^3, and, to a less degree, the ends of A^3 and C^3, are displaced in the same direction; that is, the whole animal pole moves toward the micromere end of the egg. At the same time the cells A^3, B^3, and C^3 are slightly compressed dorso-ventrally. This is the beginning of that peculiar rotation of the blastomeres in the eggs of Rotifera, described by Zelinka ('91) and others, which eventually results in the process of gastrulation.

C^3 divides next, the cleavage being equal; the products are $c^{4.1}$ and $c^{4.2}$.

Before the cleavage is finished in D^3 and C^3, spindles have been formed in B^3 and A^3, division taking place in them in the order named. The cleavage is equal, as in C^3.

The order of cleavage, then, for the four cells, is as follows: *D*, *C*, *B*, *A*. This rhythm reappears in later cleavages.

The third cleavage is therefore equatorial, dividing the egg into two layers of four cells each. The ventral cells are $a^{4.1}-d^{4.1}$, the dorsal cells $a^{4.2}-d^{4.2}$. The egg is still slightly unsymmetrical.

Views of the eight-cell stage are shown in Figures 15 to 18.

From a cyto-mechanical standpoint, the third cleavage may be characterized as follows. The first division of the asters is along a line at right angles to the axis of the previous spindles, and indicates the position of the spindles for the next cleavage. These lie in the long axes of the cells, and the cell walls are formed in the position demanded by the principle of least surfaces.

Fourth Cleavage.

Immediately after the division of D^3 (Plate **2**, Fig. 12), the asters in $d^{4.1}$ and $d^{4.2}$ begin to extend laterally, at right angles to the axis of the preceding spindles, and each becomes divided into the two asters for the following spindle. In $d^{4.1}$, Figure 11, the two asters for the succeeding cleavage are still connected by a striate band. Figure 11 shows a ventral view of the same egg as Figure 12, the five-cell stage. The corresponding dorsal view of a slightly later stage is shown in Figure 14. The asters in $d^{4.2}$ are moving apart in the same manner as in $d^{4.1}$, save that the line of separation is slightly oblique, the left aster being higher.

In the same way the asters in the cells $a^{4.1} - c^{4.1}$ and $a^{4.2} - c^{4.2}$ become constricted, and divide at right angles to the axis of the preceding spindles. The dividing asters in $c^{4.2}$ are shown in Figures 14 (Plate **2**) and 17 (Plate **3**), and those of $c^{4.1}$ in the latter figure. Views of the other four cells would show similar conditions.

From the manner in which the asters separate in all of the eight cells, one would be led to expect that the next cleavage would be meridional, at right angles to the third cleavage. This expectation is strengthened by the fact that the *lateral* dimensions of the cells in which the asters lie are considerably greater (in the quadrants *A*, *B*, and *C*, at least) than the opposite measurements (Fig. 17).

But in a slightly later stage it is observed that the line joining the asters in $d^{4.1}$ has become oblique, like that joining those of $d^{4.2}$ (as mentioned above). This oblique position of the asters in $d^{4.1}$ is shown in the ventral view (Fig. 15). The left aster (right side of the figure) has become ventral, the right one dorsal. The sagittal section (Plate **1**, Fig. 7) of a slightly later stage shows the completion of the rotation thus begun; the line connecting the two asters and passing through the nucleus is now approximately dorso-ventral in direction.

At the same time a similar rotation has taken place in the cell $d^{4.2}$, but the position taken by the two asters is not the same as in $d^{4.1}$. One of the two asters has become central, the other peripheral, as if the cell were about to divide into a deep and a superficial portion. This condition also is shown in the sagittal section, Figure 7. The difference in the position of the asters in $d^{4.1}$ and $d^{4.2}$ is apparently due to simple mechanical conditions, — the form of the cell $d^{4.2}$ compelling the asters to take the position which they have.

At the same time a slight differentiation in the cytoplasm of the cell $d^{4.1}$ becomes visible. As previously stated, the fine yolk granules are at first distributed uniformly throughout the egg. In this eight-cell stage, a slight concentration of the yolk granules in the ventral part of the cell $d^{4.1}$ may be noticed by careful observation. The condition at this time is shown in Figure 7; in the ventral part of $d^{4.1}$ the yolk granules are a little larger and more numerous. As will be shown, this concentration of yolk becomes later much more marked, and its history is peculiar.

A spindle is now formed in $d^{4.1}$ in the position indicated by the asters of that cell in Figure 7, — that is, with a dorso-ventral axis, — thus prefiguring another *equatorial* cleavage. The spindle is shown in Plate **2**, Figure 16.

Immediately thereafter the spindle is formed in $d^{4.2}$, and it appears that the position of the asters shown in Figure 7 (Plate **1**) is *not definitive*. The asters shift, so that the spindle in $d^{4.2}$ is dorso-ventral, like that in $d^{4.1}$, as is shown in Figure 16. Which of the two asters seen in Figure 7 becomes dorsal and which ventral, I have been unable to determine. During the formation of the spindle in $d^{4.2}$ the cell extends a little in the direction of the spindle, as is shown by a comparison of Figure 7 with Figure 16.

Meanwhile, changes have been occurring in the quadrants *A*, *B*, and *C*. As the processes are the same in all three, the quadrant *C* will be selected as a type.

At first, as described above, the asters separate tangentially, at right angles to the axis of the previous spindle (Plate **3**, Fig. 17). This position is retained for some time, but in a later stage the line connecting the asters in $c^{4.2}$ has become oblique, as shown in Figure 18, which exhibits a side view of the egg of which Figure 7 is a section. The asters in $c^{4.1}$ still retain their original position.

Now follows the cleavage of the cell $d^{4.1}$. This is accompanied by an increase of the dorso-ventral extent of the two products, as compared with that of the original cell. The division is unequal; the ventral cell $d^{5.1}$ is much the larger, and retains the whole of the territory containing the larger yolk granules shown in Figure 7. The larger derivative retains its position at the macromere end of the egg (Fig. 19). The smaller cell $d^{5.2}$ is therefore pushed dorsad, and this, together with the extension of $d^{4.2}$ at the time of the formation of its spindle, displaces the animal pole, marked by the polar cell, still farther toward the micromere end of the egg. As a further result, the cells of the quadrants *A*, *B*, and *C* are still more compressed dorso-ventrally, so that, especially in $a^{4.1}-c^{4.1}$, the lateral extent is much greater than the dorso-ventral (Fig. 19).

Nevertheless, as Figure 19 shows, the rotation of the future spindle axis still continues. The line joining the asters becomes dorso-ventral first in the dorsal cells $a^{4.2}-c^{4.2}$, while in $a^{4.1}-c^{4.1}$ the asters are still oblique, as shown in $c^{4.1}$, Figure 19. In quadrant *B* of this same figure, the axis has become dorso-ventral in both cells.

Now occurs the cleavage of $d^{4.2}$, with still further elongation, shifting of the animal pole toward the micromere end of the egg, and resulting greater compression of the cells of the quadrants *A*, *B*, and *C* (Figs. 20–24). Without regard to this, the asters in the cells of these quadrants continue their movements until the future spindle axes are in every case dorso-ventral. Spindles are now formed in all of the six cells, the spindle being in every case in the shortest axis of the cell (Figs. 20–24).

The conditions at this stage are so significant from a cyto-mechanical standpoint, that I have thought it best to analyze and illustrate with especial fulness a typical egg at this stage. Figures 20–25 are views of a single egg. Figure 20 shows the right side (quadrant *C*), Figure 22 the left side (quadrant *A*), Figure 21 an anterior view (quadrant *B*), and Figure 25 a posterior view (quadrant *D*). In Figures 23 and 24 are given respectively sagittal and frontal optical sections, for comparison with the surface views.

In order to exclude possibility of error, the egg from which the above figures were taken was moved about so that the six cells belonging to the quadrants *A*, *B*, and *C* occupied successively the middle of the upper surface of the egg; careful camera figures of each cell were made in this position. Then optical sections were taken in the same way, both along the axis in which the spindles lie, and at right angles to these. Accurate measurements of the dimensions of the cells could thus be made; the results are as follows.

Cell.	Dorso-ventral Measurement.	Lateral Measurement.	Ratio of Dorso-ventral to Lateral Measurement.
$a^{4.1}$	25μ (20μ[1])	52μ	1 to 2 (about) (2 to 5[1])
$a^{4.2}$	35μ	50μ	7 " 10
$b^{4.1}$	24μ	42μ	4 " 7
$b^{4.2}$	35μ	42μ	5 " 6
$c^{4.1}$	30μ	49μ	3 " 5 (about)
$c^{4.2}$	33μ	52μ	2 " 3 (about)

After the spindles become completely formed, the cells begin to elongate in the direction of the spindles. A slightly later stage than that just described is shown in Plate **4**, Figure 26. Comparing this with Plate **3**, Figure 22, it is evident that the cell $a^{4.1}$ has stretched in the direction of the spindle to such an extent that the difference between the two axes of the cells is much diminished. Nevertheless, in both this cell and $a^{4.2}$ the axes in which the spindles lie are distinctly the shorter. This is still true at the time of the division of the cells. Figure 27 (Plate **4**) shows the right side of the egg last considered; in the quadrant *C* the processes are much more advanced than in *A*. The nuclei have separated and the cytoplasm is dividing, yet exact measurements both of surface views and optical sections show that the greater diameter is still at right angles to the line joining the two nuclei. A frontal section, showing the greatest dorso-ventral extent of the cells of the quadrants *A* and *C* of this egg, is given in Figure 28.

The two figures last mentioned show another fact of importance. The divisions do not separate the blastomeres into cells of equal size in the quadrants *A*, *B*, and *C*. The completed cleavage is shown in Plate **4**, Fig. 30 (anterior view). This, with the figures just cited, shows that the cells $a^{4.2} - c^{4.2}$ divide very unequally, the dorsal derivatives, $a^{5.4} - c^{5.4}$, being very much larger than the ventral ones, $a^{5.3} - c^{5.3}$. The inequality is less in the division of the ventral cells $a^{4.1} - c^{4.1}$. Although the ventral derivatives, $a^{5.1} - c^{5.1}$, occupy a larger area on the surface of the egg, there is little difference in actual volume, and such as occurs is in favor of the more dorsal cells $a^{5.2} - c^{5.2}$.

The order of division is the same as in the last cleavage; first, the quadrant *D*, then in order *C*, *B*, *A*. In quadrant *D* the larger cell $d^{4.2}$ divides first; in the other quadrants the cells are of equal size and divide at the same time.

The important facts in this fourth cleavage, from a cyto-mechanical standpoint,-may be summarized as follows.

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[1] In every case the first measurement was taken through the two asters; in the case of $a^{4.1}$ the real dorso-ventral extent of the cell, into which the spindle later moves, is but 20μ, — so that the ratio is as two to five.

The asters in all of the eight cells after the third cleavage separate tangentially, at right angles to the direction of the preceding spindles. Having taken up positions on opposite sides of the nucleus, in every case the complex of nucleus and asters *rotates* in such a way as to bring the axis of the forming spindle into the same direction as that occupied by the spindle for the preceding cleavage. In six of the cells, this rotation is from a previous position in the *longer* axis of the cell to a later position in the *shorter* axis. In these six cells spindles are completed in the shortest axes of the cells, and division ensues in such a way that the newly formed septa are surfaces of *greatest area*, and the cells separate in the direction of *greatest pressure*.

The cleavage in $a^{4.2} - c^{4.2}$ and in $d^{4.1}$ is markedly unequal.

In two cells of equal ages but unequal size ($d^{4.1}$ and $d^{4.2}$) the larger divides first.

The exact changes in form during the divisions of the cells is a point worthy of careful attention. As the transformation of the nucleus giving rise to the spindle takes place, the cell elongates slightly in the direction of the spindle. (Compare $c^{4.1}$, Figure 24, with the earlier stage of the similar cell $a^{4.1}$ in the same figure.) As the spindle narrows and lengthens and the chromosomes begin to separate, the cell continues to elongate (Fig. 26, $a^{4.1}$, compared with Fig. 20, $c^{4.1}$, and Fig. 22, $a^{4.1}$). As the two new nuclei are formed and move apart, and the cytoplasm becomes constricted, there is a still further extension of the cells in the direction of the spindle. (Compare $c^{4.1}$ and $c^{4.2}$ with $a^{4.1}$ and $a^{4.2}$, in Plate **4**, Fig. 28.)

As Heidenhain ('94^a, p. 154) has recently urged, this elongation of the cell in the direction of the spindle is a point of great importance for a proper understanding of the conditions affecting the direction of cell division. In many later divisions in Asplanchna the spindle is first formed, as will be shown, in the short axis of the cell, and then this axis by stretching becomes the longer. It is possible that to this phenomenon is due the apparent general agreement of normal cleavage with the law of Hertwig, and that careful observation will in many cases, as in Asplanchna, show the so called law to be of little significance.

A full discussion of the bearing of the facts above described is reserved until later cleavages have been examined.

The foregoing description is based on a study of forty-two specimens from different individuals, showing the various phases of the fourth cleavage; that is, each containing more than seven and less than sixteen cells.

This cleavage, as described above, differs in some respects from that of Callidina as described by Zelinka ('91). A discussion of the differences will be found in Part Second.

The cleavage of Asplanchna priodonta takes place to this stage in exactly the same manner as that of Asplanchna Herrickii. Figure 29 (Plate **4**) shows the egg of Asplanchna priodonta in the 10-cell stage.

Fifth Cleavage.

As a basis for an account of the following cleavage, it will be well to summarize the divisions which have already taken place, and to take a careful survey of the structure of the egg at the end of the fourth cleavage.

The first and second cleavages pass through both animal and vegetative poles and are therefore meridional. The third cleavage is at right angles to the dorso-ventral axis and is therefore equatorial. The fourth cleavage is parallel to the third, thus likewise equatorial.

As a result of these cleavages, the egg now consists of sixteen cells, arranged in four dorso-ventral rows or *quadrants*, each quadrant consisting of four cells derived from one of the four blastomeres of the four-cell stage (Plates **4** and **5**, Figs. 30–36). Passing from the ventral side dorsad, we may also distinguish four *layers* of cells, each layer containing one cell of each of the four quadrants. The layers may for convenience be numbered; I will call the ventral the *first* layer, the others following in order to the *fourth*, which is at the animal pole. As a result of the shifting during cleavage, the animal pole has now come to be situated almost exactly at the micromere end of the egg; the opposite end is occupied by the large cell $d^{5.1}$ (Figs. 30 and 33, anterior and posterior views respectively). The dorso-ventral axis therefore now coincides with the long axis of the egg.

Of the four quadrants, three, *A*, *B*, and *C*, are alike in the size and arrangement of the cells of which they are composed. (See Fig. 30, anterior view.) The four cells composing any given one of these quadrants differ in size. The cell of the fourth layer (next to the animal pole) is much the largest, while that of the third layer is much the smallest. The cells of the first and second layers are nearly equal in size; that of the first layer covers more of the surface of the egg (Fig. 30), but that of the second layer is deepest (Fig. 32). The cells of the first, second, and third layers are much compressed dorso-ventrally, so that the lateral dimensions of the cells are at least twice as great as the dorso-ventral dimensions. In the third layer especially, the cells are deformed by the pressure to such an extent that the surface area exposed resembles the section of a biconvex lens. In the dorsal layer the compression is less; the cells are triangular in surface view, and the dorso-ventral extent is greatest.

All the cells of quadrant *D* are much larger than the corresponding cells of the other quadrants (Figs. 31 and 33). The ventral blastomere, $d^{5.1}$, is much the largest cell of the egg, and occupies the entire ventral end at this period. Its position as shown by the section (Fig. 32) is worthy of careful attention. Its dorsal or inner surface, like the outer, is convex; anteriorly the cell is partly covered by the ventral cells of the other quadrants, while the ventral end of cell $d^{5.2}$ extends a slight distance ventrad of the middle dorsal portion of $d^{5.1}$.

The cell $d^{5.1}$ is distinguished from all the others by a further peculiarity. I have shown above (page 25 and Fig. 7) that in the eight-cell stage there is a slight concentration of yolk material in the ventral region of the cell $d^{4.1}$, where the yolk granules are a little larger and more numerous. At the division of $d^{4.1}$, this cloud of granules, as a natural result of its position, remains in the cell $d^{5.1}$ (Plates **2** and **3**, Figs. 16 and 19). At the same time it becomes more distinctly differentiated. The granules composing the cloud increase in size and range themselves about the periphery of the egg, next to its free surface (Figs. 23, 24, Plate **3**, and Fig. 28, Plate **4**). A narrow strip of the posterior margin of the free surface of the cell is without the granules (Figs. 20, 22, and 23). At a time when the fourth cleavage is entirely completed, the granules have withdrawn still farther from the posterior margin of the cell, and show a tendency to concentrate at the free surface of the cell over its anterior half (Plate **4**, Fig. 32). In the other cells, and in the remaining portions of $d^{5.1}$, the original finely granular cytoplasm is retained, so that I have not thought it necessary to represent in the figures the yolk conditions in any region except where the cloud of granules is present.

The cell of the second layer, $d^{5.2}$, is next in size, then the dorsal cell, $d^{5.4}$, while the cell of the third layer is the smallest in quadrant *D*. The cells $d^{5.2}$ and $d^{5.3}$ are very greatly compressed dorso-ventrally and elongated laterally, so as to form irregular flat plates, extending from the posterior surface of the egg two thirds of the distance to the anterior surface. (Compare Figure 31, left posterior surface, with Figure 32, section.) The dorsal cell $d^{5.4}$ is likewise compressed dorso-ventrally, so as to appear in a sagittal section (Fig. 32) as a low triangle.

As a whole, the form and arrangement of cells are far from what is demanded by the principle of least surfaces. Flat plates, such as we see in $d^{5.2}$ and $d^{5.3}$, and in all the cells of the third layer, retain their form in virtue of some force working strongly *against* surface tension.

After the fourth cleavage, the asters in all the cells at first separate at right angles to the axes of the preceding spindles, as happened after the third cleavage. The later changes are essentially the same in all the quadrants, so far as the asters are concerned, so that quadrant *D* may be described as a type.

Figure 31 (Plate **4**) shows the conditions in the four cells of quadrant *D*, after the asters have divided. The two asters of each cell lie upon opposite sides of their nuclei in such a position that, if no change occurs, the ensuing division will be meridional.

In the cells of the first three layers the asters retain their original positions. But in $d^{5.4}$ a rotation takes place, such as occurred in all the cells in preparation for the preceding (fourth) cleavage, so that the axis of the spindle in $d^{5.4}$ is at right angles to the axes of the spindles in the other three cells of the quadrant. This condition is shown in Figure 33, and the completion of the division is shown in Plate **5**, Fig. 37.

The same processes take place in the other quadrants, so that all the cells of the first three layers have spindles extending laterally, while in the fourth or dorsal layer the spindles are directed dorso-ventrally (Fig. 40).

We must now consider the cleavage in the several cells more in detail.

As in previous cleavages, division takes place first in the cells of quadrant *D*. The nucleus of the large ventral cell, $d^{5.1}$, is earliest to enter upon the karyokinetic process, followed immediately by $d^{5.2}$, and a little later by $d^{5.3}$ and $d^{5.4}$. Figure 33 (Plate **4**) gives a view of the posterior surface of the egg at this stage, showing the spindles in all the cells. As this figure shows, the spindles in the three cells $d^{5.1}$, $d^{5.2}$, and $d^{5.3}$ do not lie in the middle of the cells, but nearer the right ends. (See definition of right and left, page 17.) In the dorsal cell, $d^{5.4}$, the spindle is at right angles to those in the other cells. The plane of cleavage indicated in the three ventral cells is meridional; in the dorsal cell it is equatorial, like that of the two preceding cleavages. The division of each of the four cells must be considered separately.

To understand the cleavage of the large ventral cell, $d^{5.1}$, it is necessary to observe accurately its position and relation to the other cells. A longitudinal section of about the same stage as that shown in Figure 33 is given in Figure 34. Comparing this with the earlier corresponding section, Figure 32, it is seen that with the formation of the spindles in $d^{5.2}$ and $d^{5.3}$ these cells have yielded to the well known tendency to take a more rounded form at the time of karyokinesis; the inner parts of the cells have been withdrawn toward the surface and used in increasing the dorso-ventral dimensions of the cells. The animal pole has been thereby pushed still farther in the direction in which it has been steadily migrating, so that it is actually past the micromere end of the egg. The cells of the quadrants *A*, *B*, and *C*, being in a "resting" condition, give way to the compression, and become much deeper and flatter than before. The cell $d^{5.1}$ retains its position at the macromere end of the egg, but lying in a concavity, partly surrounded by the other cells. The spindle lies in the deeper (more dorsal) parts of the cell, with its right end (Fig. 33) deepest, and close to the wall of the cell. A view from the ventral end of the egg (Plate **5**, Fig. 35) shows that this "right" end is really anterior, and that the spindle lies in an antero-posterior plane, coincident with the plane separating the quadrants *A* and *B*. The anterior (inner) end of the spindle lies close against the boundary between $a^{5.1}$ and $b^{5.1}$.

The division which now ensues is of an extraordinary character. The anterior end of the spindle is pressed against the periphery of the cell at the place above mentioned, and a minute vesicle is given off, which lies embedded between the cells $a^{5.1}$ and $b^{5.1}$. This, after the division is finished, is shown in Figure 38 (Plate **5**), the vesicle being labelled $d^{6.2}$.

During division, the granular cloud which was described as occupying the anterior half of the periphery of the cell moves still farther toward the anterior margin, and shows a tendency to concentrate into a more definite group; the individual granules become larger also (Fig. 38).

In $d^{5.2}$ and $d^{5.3}$ the spindles are parallel to the spindle in $d^{5.1}$, the right ends being nearer the boundary of the cells, and deeper within the egg. The latter fact is shown in the transverse section, Figure 36, passing through the cells of the third layer. The divisions are unequal, as foreshadowed by the position of the spindles, but the inequality is much less than in the case of $d^{5.1}$. The completed division is shown in Figure 37. The cleavage takes place first in $d^{5.2}$.

At about the same time as the division of $d^{5.3}$ occurs that of the dorsal cell, $d^{5.4}$. Here the spindle is in the short axis of the cell; the cleavage is equatorial and unequal, the dorsal cell being much the smaller (Fig. 37).

During the occurrence of the cleavage of these cells other changes, which are of the greatest importance, have been taking place, partly as a consequence of these cleavages. As the constriction of the cytoplasm in $d^{5.2}$ and $d^{5.3}$ occurs, these cells show in a most pronounced way the tendency to become of a rounded form. The inner portions of the cell are withdrawn still more from the centre of the egg, until the antero-posterior measurements are no greater than their dorso-ventral dimensions. This is shown in the section, Figure 38. In this egg, a surface view of which is given in Figure 37, the cleavage of $d^{5.2}$ is finished, and the products, $d^{6.3}$ and $d^{6.4}$, have already passed into the "resting stage," so that they take whatever form is impressed upon them by the surroundings. But $d^{5.3}$ is just dividing into $d^{6.5}$ and $d^{6.6}$, and the form shown in section by $d^{6.5}$ in Figure 38, as compared with the form of $d^{5.3}$ in Figure 32, shows the change which I have been describing.

At the same time the cells of the other quadrants, *A*, *B*, and *C*, are entering upon the stages preparatory to karyokinetic division. As a first step they also retract their deeper parts and bring their protoplasm into a more compact mass, as shown by a comparison of quadrant *B* in Figure 34 (Plate **4**) with the similar quadrant, *A*, in Figure 38 (Plate **5**).

As a consequence of this withdrawal of material from the inner parts of the egg, the large ventral cell $d^{6.1}$, which has now passed into the resting stage, moves inward to occupy the space which would otherwise be vacant, — being forced to do so, of course, by the greater dorso-ventral extension of all the other cells. The result is shown in Figure 38. This partial enclosure of $d^{6.1}$ by the other cells is of course a stage in the process of gastrulation.

Before the cleavage of all the cells of quadrant *D* is finished, the karyokinetic processes have begun in the other three quadrants. (See Plate **5**, Figs. 39–42.) The first cells to show the characteristic nuclear phenomena are those of the fourth or dorsal layer, $a^{5.4} - c^{5.4}$. As previously stated, the asters at first take up such a position in these cells as would lead, if unchanged, to a meridional cleavage. But in these three cells, as in $d^{5.4}$, there is a revolution of the asters and nuclei, resulting in a dorso-ventral position of the spindles. At any given period the three cells are not in exactly the same phase of division, though very nearly so; the order, beginning with the most advanced, is $c^{5.4}$, $b^{5.4}$, $a^{5.4}$. The sequence is thus the same as in previous cleavages. The division is equatorial and the dorsal product is the smaller, as in the cleavage of the corresponding cell ($d^{5.4}$) of the left posterior quadrant. In the three cells of quadrants *A*, *B*, and *C* the spindles are not in the short axes, as in $d^{5.4}$, since these cells are not nearly so broad as that one, while the dorso-ventral dimension is about the same or greater (Plate **4**, Figs. 30 and 32). Figure 41 (Plate **5**) shows the process of cleavage in these cells, while Figure 45 (Plate **6**) shows the cleavage concluded.

The division of the second layer follows upon that of the fourth, and again in the order $c^{5.2}$, $b^{5.2}$, $a^{5.2}$. The division is here meridional, as it is in the corresponding cells of the quadrant *D*, and equal, as it is *not* in the corresponding cell of the quadrant *D*. (See Figs. 39, 40, 43, and 44.)

Next follow the divisions of the cells of the first layer, in the same order as in the previous cleavages, and, slightly later, the divisions in the third layer, also in the same sequence. The cleavages here also are meridional and equal.

The nuclear conditions leading to these cleavages are shown in Figures 39, 40, 42 (Plate **5**), all from the same egg. A somewhat later stage is shown in Figure 43, which exhibits the conditions in the quadrants *A*, *B*, and *C* at a time when the divisions just described are completed in most of the cells. All the divisions are nearly finished except in the cells of the third layer ($a^{5.3} - c^{5.3}$), which still contain spindles. This view shows also another peculiar fact. During the cleavages the cells about the dorsal pole of the egg have shifted, and the cells $a^{6.7}$ and $c^{6.7}$ have pushed ventrad to such an extent that on the right side the cells $c^{5.3}$ and $b^{5.3}$ have become completely separated, a part of the cell $c^{6.7}$ lying between them. This condition is only transitory, however; the cell $c^{6.7}$ is very soon pushed dorsad again, and the cells of the third layer again form a continuous row. (Compare Figure 47, Plate **6**.) Figure 46 shows the cells of the quadrant *D* at the close of this division, while Figure 45 is a view of the animal pole at the same stage.

The features of the fifth cleavage may be summarized as follows. In the twelve cells of the three ventral layers, the asters separate after the fourth cleavage at right angles to the position of the preceding spindles and retain the position first taken; the cleavage is therefore meridional. In all these cells the spindles are in the long axes of the cells. In the dorsal layer the asters at first assume the same position as in the other cells, but later a rotation takes place, and the spindles when formed have a dorso-ventral direction; the resulting division is equatorial. The spindle is in the longer axis of the cells $a^{5.4}$, $b^{5.4}$, and $c^{5.4}$, in the shorter axis in $d^{5.4}$.

The division is unequal in the four dorsal cells of all the quadrants, and in all the cells of the quadrant *D*. In the other cells it is equal.

The sequence of cleavage is the same as in previous divisions, but with some modifications. In any given layer of cells, the order is *D*, *C*, *B*, *A*; a repetition of the sequence established at the third cleavage. In any given quadrant, the order of cleavage varies with the relative size of the cells. In the quadrant *D* the order is (beginning with the ventral cell) 1, 2, 4, 3, and this is also the order of relative size of the cells, beginning with the largest. In the other quadrants the order of cleavage is 4, 2, 1, 3, and this again is the order of comparative size beginning with the largest, except that 2 and 1 are so nearly of a size that it is difficult to say from observation that either is the larger.

The fifth cleavage is accompanied, as a result of the changes in form of the cells during karyokinesis, by a partial enclosure of the ventral cell of quadrant *D* ($d^{6.1}$) by the other cells.

The above account of the fifth cleavage is based upon an examination of twenty-five eggs, taken from different individuals and showing different phases of the division; i. e. each egg contained more than fifteen and less than thirty-two cells.

Sixth Cleavage.

The first division belonging to the sixth cleavage, that of $d^{6.1}$, takes place coincidently with the last division of the fifth cleavage, that of $a^{5.3}$. There is thus no resting period between the two cleavages. Nevertheless, there is a sufficiently well characterized stage of thirty-one or thirty-two cells, just as the cleavage of $d^{6.1}$ occurs, and it will be well to describe the egg in this condition as a basis for an account of the sixth cleavage.

Figure 43 (Plate **5**) shows the anterior surface just before this stage is attained; Figure 47 (Plate **6**) shows nearly the same surface after the fifth cleavage is finished. The posterior surface is shown in Figures 46 (Plate **6**), 53, and 54 (Plate **7**); the animal pole, in Figure 45 (Plate **6**). Figure 48 shows a sagittal section, while a transverse section of a stage just later (looking toward the animal pole) is given in Figure 52.

The principal axis of the egg still coincides with its long axis, the animal pole lying at or near the micromere end, the vegetative pole at the macromere end (Fig. 48).

The egg now consists of (1) a single large cell, $d^{6.1}$, embedded within the other cells and appearing on the surface at the ventral end only (Plate **5**, Fig. 38), and (2) of thirty-one smaller cells, partly surrounding the larger cell $d^{6.1}$. One of these smaller cells, $d^{6.2}$, is a minute vesicle embedded between the cells $a^{5.1}$, $b^{5.1}$, and $d^{6.1}$ (Figs. 38 and 42).

The other thirty cells show a regular arrangement. The four quadrants may be distinguished as at the beginning of the fifth cleavage, each quadrant now containing eight cells, showing a characteristic arrangement. From ventral to dorsal we may now distinguish five layers. The first three layers contain each eight cells, two from each quadrant. In the quadrants *A*, *B*, and *C*, the two cells of a given layer are equal (Plate **6**, Fig. 47). In quadrant *D* there is great irregularity. The two cells of the ventral layer are extraordinarily unequal, constituting the large partly interior cell $d^{6.1}$, and the minute vesicle $d^{6.2}$, also enclosed within the other cells (Plate **5**, Fig. 38). In the second and third layers the two cells are likewise unequal, though less markedly so.

The fourth layer consists of a single large cell from each quadrant; that of quadrant *D* being the largest (Plate **6**, Fig. 45).

The fifth layer consists of four small cells at the dorsal pole of the egg (Fig. 45). The arrangement at the animal pole formed at the four-cell stage (Fig. 8) is still maintained. The quadrants *B* and *D* are in contact for a considerable distance, whereas *A* and *C* do not touch. In one of the points where three cells of different quadrants meet (in this case $b^{6.8}$, $c^{6.8}$, and $d^{6.8}$) lies the polar cell.

The first cells in which indications of cleavage are observed are again the large cells of the *D* quadrant, $d^{6.1}$ and $d^{6.3}$. Spindles are formed in these at about the same time (Plate **6**, Fig. 48). The processes taking place in the two cells differ, and must be considered separately.

In $d^{6.1}$, after the giving off of the small vesicle $d^{6.2}$, the nucleus very quickly enlarges to its original size. The aster begins to elongate at right angles to the position of the previous spindle (Plate **5**, Fig. 38). But at almost the same time a rotation takes place, and by the time the two asters are fully separated the line connecting them is seen to be nearly antero-posterior (Plate **5**, Fig. 42). The movement continues until the axis of the complex becomes exactly antero-posterior, and a spindle is formed *in precisely the same position as the spindle for the preceding cleavage.* This spindle is shown in the sagittal section, Figure 48. Its anterior end lies just ventrad of the small vesicle formed at the previous cleavage. Division now takes place, and a *second* small vesicle is given off to the point in the median plane lying just ventrad of the vesicle formed at the fifth cleavage. Figure 49 shows the process of formation of this vesicle, and Figure 50 shows the condition of affairs after the division is finished. In later stages the two vesicles are visible, lying beneath the cells of quadrants *A* and *B*, in the place where they were given off. (Compare Figure 50, Plate **6**, with Figures 56, Plate **7**, and 65, Plate **8**.)

Other changes occur at the same time in the large ventral cell. After the fifth cleavage the granular cloud in the cytoplasm gathered into the region of the anterior margin of the free surface of the cell (Plate **5**, Fig. 38). As the spindle for the sixth cleavage is formed, the cloud becomes concentrated over a small area, at a slight distance from the anterior margin of the cell (Plate **6**, Fig. 48). Then, as division takes place, the cloud moves up to the anterior margin, at the same time spreading out, and begins to pass beneath the cells of the quadrants *A* and *B* (Figs. 49 and 50). As the large nucleus moves away from the wall of the cell where the vesicle was formed, the granular cloud moves inward (dorsad) and spreads out between the nucleus of the large cell and the two vesicles (Figs. 51 and 52). The granules at this time have become very coarse and distinct.

Meantime, cleavage is taking place in the cell $d^{6.3}$. In this cell the changes occurring in the asters are peculiar.

Immediately after the preceding cleavage, the cell, having passed into the resting stage, has been pressed into an irregular wedge-shaped form by the processes occurring in the surrounding cells (Plate **5**, Fig. 37, surface view, and Fig. 38, section, from the same egg). The cell has become very narrow at the level at which the nucleus lies, so that, apparently, there is not room for the asters to separate at right angles to the foregoing spindle. The nucleus is pressed closely against the ventral wall of the cell (Fig. 38), and the aster begins to extend obliquely along the dorsal side of it, between the nucleus and the dorsal wall of the cell. When the aster has become completely divided and the products are on opposite sides of the nucleus, their common axis is already in the same direction as the axis of the spindle at the previous division. The same result is obtained as in the rotation at the fourth cleavage, though in a different manner. *But the final position is not yet reached.*

As now situated, the asters lie in the long axis of the much elongated cell (Plate **6**, Fig. 46). As the active condition preparatory to division comes on, the cell withdraws its deeper parts (shown in Plate **5**, Fig. 38), and its dorso-ventral dimension increases. Accompanying this change is a rotation of the nuclear complex, from a position with the axis in the greatest dimension of the cell, to a position with axis in the shortest dimension. This change is shown in progress in Plate **7**, Fig. 53. A later stage is shown in Figure 54; here the spindle is completely formed. The dorso-ventral axis of the cell has greatly increased, but is still distinctly less than the width of the cell at right angles to the spindle. The cytoplasm has become grouped symmetrically about the spindle, with the latter in its *short* axis. A longitudinal section of the same egg is shown in Plate **6**, Fig. 48; the completed cleavage ($d^{7.5}$ and $d^{7.6}$) is shown in section in Figure 50, and from the surface in Plate **7**, Fig. 57. The cleavage is unequal, the ventral cell being much the smaller.

Cleavage in the other cells of this generation takes place in a sequence that is complicated by various factors, so that the account will be clearer if the divisions of the cells are described in connection with their relative positions in the egg, reserving a discussion of the order of cleavage till the end. The divisions will be taken up according to the layers of cells, beginning with the ventral layer.

First or Ventral Layer, consisting of the eight cells, $a^{6.1} - d^{6.1}$ and $a^{6.2} - d^{6.2}$.

The cleavage of $d^{6.1}$ has been described. The small vesicle $d^{6.2}$ does not divide farther. The other cells of this layer divide equatorially into cells of equal size. Two of the spindles leading to this cleavage are shown in Figure 56 (Plate **7**), and the completed cleavage in Figure 61. The resulting fourteen cells are $a^{7.1} - d^{7.1}$, $a^{7.2} - d^{7.2}$, $a^{7.3} - c^{7.3}$, and $a^{7.4} - c^{7.4}$.

Second Layer, containing the cells $a^{6.3} - d^{6.3}$ and $a^{6.4} - d^{6.4}$.

The cleavage of $d^{6.3}$ has been described; it is equatorial and unequal. The remainder of the cells also divide by equatorial furrows, but the products are equal in size. One of the spindles is shown in $c^{6.4}$, in Figure 47 (Plate **6**), and in Figure 55 (Plate **7**) the nearly completed cleavage; the nuclei in all but the products of $c^{6.3}$ are still connected by interzonal filaments. The same condition of the cell $d^{6.4}$ is shown in Figure 57 (the products being $d^{7.7}$ and $d^{7.8}$). In all of these cells, except $d^{6.4}$, the spindles lie at first in the shorter axes of the cells, as indicated in Figure 47 (Plate **6**); but as the karyokinetic processes progress, the cells elongate in the direction of the spindles until the axes in which the spindles lie are the longer.

The products of this division are $a^{7.5} - d^{7.5}$, $a^{7.6} - d^{7.6}$, $a^{7.7} - d^{7.7}$, and $a^{7.8} - d^{7.8}$.

Third Layer, containing the eight cells $a^{6.5} - d^{6.5}$ and $a^{6.6} - d^{6.6}$.

In all these cells the division is meridional, not equatorial, as in the cells of the first and second layers. One of the spindles ($b^{6.5}$) is shown in Figure 55 (Plate **7**). The cleavage in $d^{6.5}$ and $d^{6.6}$ is shown in Figure 57. In this figure, $d^{6.5}$ has already divided into $d^{7.9}$ and $d^{7.10}$, the nuclei of which are still connected by interzonal filaments. In $d^{6.6}$ the spindle is still present. The completed division in the anterior part of the egg is shown in Figure 61. The cleavage is equal in all the cells of this layer except $d^{6.6}$ and $c^{6.6}$; in these it is unequal. The unequal cleavage of $c^{6.6}$ is shown in Figure 58, and the same figure shows the unequal products ($d^{7.11}$ and $d^{7.12}$) resulting from the division of $d^{6.6}$.

By the division of the third layer a band of sixteen cells is produced, extending completely around the embryo. The cells composing the band are $a^{7.9}-d^{7.9}$, $a^{7.10}-d^{7.10}$, $a^{7.11}-d^{7.11}$, and $a^{7.12}-d^{7.12}$.

Fourth Layer, containing the four cells $a^{6.7}-d^{6.7}$.

In these cells the cleavage is meridional, as in the third layer, and in every case equal. The spindles in $b^{6.7}$ and $c^{6.7}$ are shown in Figure 47 (Plate **6**).

The eight cells resulting from this cleavage are $a^{7.13}-d^{7.13}$ and $a^{7.14}-d^{7.14}$.

Fifth Layer, containing the four cells $a^{6.8}-d^{6.8}$, situated at the animal pole of the egg.

The four small cells at the animal pole of the egg divide equatorially. The spindle of $d^{6.8}$ is shown in Figure 59 (Plate **7**); and of $a^{6.8}$ in Figure 60. The cleavage products are very unequal; the dorsal cells so formed are very minute, so that the distinction between cell body and nucleus cannot be observed, and the cells cannot be distinguished from the polar cell lying in the same region. Figure 60 shows the cleavage at the animal pole completed except in the cell $a^{6.8}$. A group of three small vesicles, representing the dorsal cleavage products of the cells $b^{6.8}-d^{6.8}$, lie at the animal pole, surrounded by the four larger cells, — one of which is the undivided cell $a^{6.8}$, while the others are the ventral cleavage products of $b^{6.8}-d^{6.8}$.

The eight cells thus produced are $a^{7.15}-d^{7.15}$ and $a^{7.16}-d^{7.16}$.

This, the sixth, cleavage may be tabulated as follows: —

Layer.	Cells.	Direction of Cleavage.	Nature of Cleavage.	Product.
First, or Ventral	(a, b, c, d) $^{6.1}$ and $^{6.2}$	Equatorial (except $d^{6.1}$)	Equal (exc. $d^{6.1}$)	$(a-d)$ $^{7.1}$ and $^{7.2}$, $(a-c)$ $^{7.3}$ and $^{7.4}$ [and $d^{6.2}$].
Second	(a, b, c, d) $^{6.3}$ and $^{6.4}$	Equatorial	Equal (exc. $d^{6.3}$)	$(a-d)$ $^{7.5}$ and $^{7.6}$; $(a-d)$ $^{7.7}$ and $^{7.8}$.
Third	(a, b, c, d) $^{6.5}$ and $^{6.6}$	Meridional	Equal (exc. $c^{6.6}$, $d^{6.6}$)	$(a-d)$ $^{7.9}$ and $^{7.10}$; $(a-d)$ $^{7.11}$ and $^{7.12}$.
Fourth	(a, b, c, d) $^{6.7}$	Meridional	Equal	$(a-d)$ $^{7.13}$ and $^{7.14}$.
Fifth	(a, b, c, d) $^{6.8}$	Equatorial	Unequal	$(a-d)$ $^{7.15}$ and $^{7.16}$.

Since the minute cell $d^{6.2}$ does not divide, we thus have produced sixty-three cells instead of the typical number, sixty-four. Such a stage does not, however, have an actual existence, since some of the divisions belonging to the seventh cleavage have taken place before all these cleavages are finished.

Figure 61 (Plate **7**) shows the anterior surface of the egg at the end of the sixth cleavage, Figure 58 the posterior surface, Figure 60 the dorsal pole, and Figure 63 (Plate **8**) the ventral pole.

Sequence of the Sixth Cleavage. — The order in which the cells divide is, as I have already stated, now complicated by several factors.

(1) The divisions of the first four quadrants of the egg (at the third cleavage) were not synchronous, but followed in the order *D, C, B, A*. Other conditions remaining the same, — that is, with equal intervals between the ensuing cleavages, — the same order would obtain in the later stages.

(2) As discussed on page 35, the sequence becomes modified during the fifth cleavage, so that the cells in any given quadrant divide in nearly or quite the order of size of the blastomeres, beginning with the largest. In the three quadrants *A, B,* and *C*, the order is (the ventral cell in each case being considered number one) 4, 2, 1, 3, while in the quadrant *D* the order is 1, 2, 4, 3. This order would naturally reappear in the sixth cleavage, other conditions remaining the same.

Both the above factors do influence the fifth cleavage, but with still further complications. The first factor appears in the fact, that in any given layer the general order of cleavage of the component cells is *D, C, B, A*.

The second factor is shown by considering the cleavage of a single quadrant, as *D*. The order of cleavage for the large left hand cells of this quadrant is as follows, naming the layers from ventral to dorsal: 1, 2, $\{{}^{3}_{4}$, — nearly or quite the same as at the last cleavage.

But a third factor appears in comparing the large left hand cells $d^{6.3}$ and $d^{6.5}$ of the *D* quadrant with their small right hand sister cells $d^{6.4}$ and $d^{6.6}$ (Plate **5**, Fig. 37, Plate **6**, Fig. 46, Plate **7**, Figs. 54 and 57). *The large cells of each pair divide first*, though the age of the two, being sister cells, is exactly the same.

Similar relations may be shown for the other quadrants. Two facts are worthy of particular notice. (1) The large cells $a^{6.7} - c^{6.7}$ divide first of all the cells in the quadrants *A, B,* and *C*, — and long before the small cells $a^{6.8} - c^{6.8}$, which are of exactly the same age. (2) There are some variations which cannot be brought into relation with any of the factors mentioned. Thus, Figure 56 (Plate **7**) shows that the cell $b^{6.1}$ is dividing before the cells $c^{6.1}$ and $b^{6.2}$, though the cells are apparently of the same size, and from the sequence of preceding cleavages the cell $c^{6.1}$ would be expected to divide first. However, such variations *may* be correlated with differences in the size of the cells, since it is impossible to calculate precisely the volume of cells which have such irregular forms, and are subjected to varying conditions with the changing positions of the surrounding cells.

Certain general facts appear from the preceding discussion of the sixth cleavage. (Compare the table of this cleavage, on page 39.)

(1) Every cell of any quadrant cleaves with its spindle in the same direction as the corresponding cell of any other quadrant (except the large interior cell $d^{6.1}$).

The cleavage of a single typical quadrant up to this time is shown in the annexed diagram (Diagram I.).

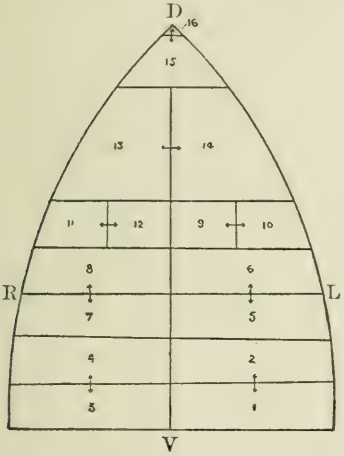

Diagram I.

Diagram of quadrant *A*, *B*, or *C* in the seventh generation. Only the second exponent designating the cells appears in the diagram, the first being in all cases 7. Thus, the cell labelled 5 represents $(a, b, \text{or } c)^{7.5}$. The arrows connect cells of common origin, and show the direction of the spindles at the preceding division. R signifies right; L, left; D, dorsal; V, ventral; according to the plan of orientation explained at page 14.

(2) All the cells in any layer (series of cells occupying the same relative position between the dorsal and ventral poles of the egg) cleave with spindles in the same direction (except $d^{6.1}$).

(3) All the cleavages are equal except in the dorsal (fifth) layer, and in $d^{6.1}$, $c^{6.6}$, and $d^{6.6}$.

(4) There is a tendency for the largest cells to cleave fastest. The minute cell $d^{6.2}$ does not cleave at all.

(5) The cell $d^{6.1}$ cleaves in such a manner as to form a marked exception to the method followed by the other cells. Its cleavage is very

unequal, while all the other cells in the ventral layer cleave equally. Also, the spindle does not lie in the same direction as in the other cells of this layer.

The exceptional nature of the division in $d^{6.1}$ evidently demands explanation. The regularity of the cleavage in the other cells of the egg is such that some special condition must be correlated with the markedly differing division of this cell. The cleavage of $d^{6.1}$ differs from that of the other cells of the ventral layer in the following points. (1) Its cleavage is very unequal, while the cleavage of the other cells is equal. (2) The spindle for the sixth cleavage in $d^{6.1}$ lies in almost exactly the same position as did the spindle for the preceding cleavage, whereas in the other cells of the ventral layer the spindle for the sixth cleavage is at right angles to the position of the spindle for the fifth cleavage.

As to the first point, — that of unequal division, — no special correlating factor for *this* particular case seems necessary, since in many cases in this and preceding cleavages the cells varied as to the equality of the division, though alike in other respects. Thus, in the fifth cleavage, the three ventral cells of the *D* quadrant cleft unequally, though in all the other quadrants the division was equal; and in this sixth cleavage the cells $c^{6.6}$ and $d^{6.6}$ divide unequally, though in all the other cells of the same layer the division is equal.

But the second point is totally exceptional in the cleavage up to this time. The axial relations of the cells appear to be so distinct and constant, and there is such uniformity in the positions of spindles at a given cleavage among cells of similar origin and relative position, that one must look for some other marked difference in the cell $d^{6.1}$ that might occasion this change of axis.

In what respects does the cell $d^{6.1}$ differ from the other cells of the egg? (1) In its greater size; (2) in its position.

(1) The greater size evidently has nothing to do with the different direction of cleavage, since the same disparity in size was present in earlier cleavages, yet this cell divided in the same direction as did the other ventral cells.

(2) The change of position is such as to bring about a fundamental change in the relations of the cell to the egg as a whole and to the other cells. Previously the cell $d^{6.1}$ formed the posterior cell of the ventral layer. At the time of the sixth cleavage the cell has moved toward the interior of the egg and its posterior surface is covered as far ventrad as its anterior surface. The cell is now *central*, and surrounded

on all sides by other cells. It thus occupies a position in the egg which is fundamentally different from that occupied by any other cell. Correlated with this fundamentally different position, the cell acquires a fundamentally different method of division.

It is impossible to say whether any particular feature of the different position of the cell is the essential one in bringing about this altered method of cleavage. As the cell moves inward, it very probably accomplishes a partial rotation (see below); if the axes of the cell are definite, and *determined within the cell alone*, then this rotation would cause a change in the position of the axes of the cell $d^{6.1}$ in comparison with the axes of the other cells, and a different direction of the spindle would result. But any such explanation is hypothetical.

During the later stages of the sixth cleavage, the process of *gastrulation* has made much progress. At the end of the fifth cleavage the large ventral cell $d^{6.1}$ had already moved some distance toward the interior of the egg (Plate **5**, Fig. 38). As the cells $d^{6.3}$ and $d^{6.5}$ now withdraw successively their deeper parts and increase their surface extension during division, they push ventrad, displacing the posterior part of the ventral cell (now $d^{7.1}$). (Compare Plate **6**, Figs. 48, 50, and 51.) The large cell therefore pushes dorsad into the interior of the egg, occupying the space made vacant by the ventral extension of the other cells. Soon after, the anterior cells, belonging to quadrants *A*, *B*, and *C* also enter upon the karyokinetic process, and in so doing likewise push ventrad (Plate **8**, Fig. 64) at the same time vacating of course a portion of the space before occupied by them near the animal pole. The cell $d^{7.1}$ therefore continues to move dorsad, so that at the end of this cleavage it is almost completely enclosed (Fig. 65).

During this inward movement of the cell $d^{7.1}$, the cloud of granules previously described changes its position still further. We had traced it, after the sixth cleavage, until it occupied a position between the nucleus of $d^{7.1}$ and the two vesicles formed at the fifth and sixth cleavages (Plate **6**, Fig. 51). As gastrulation continues, the cloud of granules migrates still further dorsad, and later even crosses the dorso-ventral axis, so as to lie posterior to it, surrounding the dorsal aster at the next division of $d^{7.1}$ (Plate **8**, Fig 64).

This movement of the cloud of granules *possibly* gives the key to the change of axis of division in the cell $d^{7.1}$. When the *posterior* cells extend ventrad during division, as previously described (Plate **6**, Figs. 48 and 51), they push against the posterior side of the cell $d^{6.1}$, thus displacing the cell inward. But such an impulse from one side only would naturally, if the cell be a body not entirely fluid, give it a rotary motion. As a result of the partial rotation, the cloud of granules is now found underneath the anterior cells (Plate **6**, Fig. 50). When the *anterior* cells extend ventrad, the form of $d^{7.1}$ is so changed by its change of position that the cells do not *push against* it, but glide over it, at the same time vacating a part of the dorsal region of the egg (Plate **8**, Fig. 64). Therefore the cell $d^{7.1}$, as it moves inward, continues its rotation in the same direction as before, and the cloud of granules is brought to the dorsal end of the cell, and even farther.

Such a rotation would explain clearly the peculiar position of the spindle in $d^{6.1}$ at the sixth cleavage. To agree with the other cells of the ventral layer, the spindle would have to take a dorso-ventral position. (Compare Fig. 55, Plate **7**.) But a rotation from posterior to anterior just before this cleavage would bring the spindle into an antero-posterior position, such as actually occurs.

However, the explanation is not very satisfactory, for several reasons. (1) We have previously seen that the granules forming the granular cloud *do* move *within the cytoplasm* of the cell, so that this change of position of the granular mass may be due to simple migration through the protoplasm of the cell. (2) A study of the movements of the asters after the fifth and sixth cleavages does not give evidence of any such rotation. (See the account of the movements of the asters before the sixth cleavage, page 36, and before the seventh cleavage, page 54.) (3) Such a rotation explains the position of the spindle at the sixth cleavage only, — while all the later cleavages of the inner cells are likewise out of relation to the divisions of the outer cells. (4) The explanation assumes that the position of the axes of cleavage is definite, and *determined within the cell itself*, so that, if the cell rotates, the axis rotates with it, — which is not proved.

The only conclusion in which we are entirely justified is therefore merely this, that as the relation of the cell $d^{6.1}$ to the other cells and to the egg as a whole becomes fundamentally changed, the method of division likewise becomes fundamentally changed.

At the close of the processes thus far described, the egg has evidently passed into the "gastrula stage" proper (Plate **8**, Fig. 64). The blastopore is still large and lies at the macromere end of the egg. It is surrounded at first by eight cells, two belonging to each of the four original quadrants of the egg (Plate **7**, Fig. 56). Later, as the sixth cleavage is entirely finished, one of the cells ($c^{7.1}$) becomes displaced and is shut out from the margin of the blastopore (Plate **8**, Fig. 63), which is itself diminished in size. The interior of the gastrula is occupied by the large cell $d^{7.1}$ and the two minute vesicles $d^{6.2}$ and $d^{7.2}$ (Fig. 64). The interior cells are surrounded by a single layer of outer cells, except at the animal pole of the egg, where the small dorsal cells do not reach to the cells within the gastrula, but lie on the surface, making here a two-layered region. This region remains two-layered as long as it is possible to trace the history of the animal pole of the egg.

The three inner cells $d^{7.1}$, $d^{6.2}$, and $d^{7.2}$, with the products of the former, may henceforth be called the *entoderm*, the outer layer the *ectoderm.*

Seventh and Later Cleavages.

I have followed the cleavage through another generation, and, for parts of the egg, much farther. It becomes impracticable, however, to describe the cleavage according to the layers or series in which it takes place, as has been done up to this stage, owing to the complicated succession of the divisions in the different cells, and to the great changes in position taking place while the cleavages are in progress. I shall therefore now describe the processes in the general order in which they occur, and in so doing I shall consider separately (1) the ectoderm, and (2) the entoderm.

THE ECTODERM.

In discussing the changes taking place in the ectoderm, it will be well to distinguish for convenience of description two regions: (1) the (left) posterior part of the ectoderm, derived from the quadrant *D;* (2) the anterior and right lateral portions of the ectoderm, derived from the quadrants *A*, *B*, and *C*. While the phenomena occurring in all of these regions are reducible to the same general scheme, so far as the method of cleavage is concerned, the irregularity in the size of the blastomeres forming quadrant *D,* their earlier cleavage as compared with the other quadrants, and the fact that some of the cells have passed inward to form the entoderm, give this region a peculiar and somewhat irregular character, which makes it convenient to discuss it separately.

(1) *The Quadrant D.* — The entoderm cells belong genetically to this quadrant, but they will be considered later.

In order to understand the conditions in quadrant *D*, and to see their relations with the arrangement in the other quadrants, it will be well to emphasize certain features of the last two cleavages.

At the fifth cleavage, as previously described, the three ventral cells of quadrant *D* divided by meridional planes into unequal portions, the left derivative being in every case larger (Plate **4**, Fig. 33, and Plate **5**, Fig. 37). The single dorsal cell divided equatorially into a small dorsal and a large ventral part. There is appended a diagram of the quadrant *D* after this cleavage (Diagram II.). If the septa in the three ventral cells were moved to the middle of the cells, the diagram would represent the condition in any one of the other three quadrants.

At the next division (sixth) the two ventral cells $d^{6.1}$ and $d^{6.2}$ have passed inward, becoming the entoderm, so that we may omit them from the present discussion. Of the other cells, the ventral pair ($d^{6.3}$ and $d^{6.4}$) divide equatorially, $d^{6.3}$ unequally, $d^{6.4}$ equally (see Plate **7**, Figs. 57 and 58). The two next layers divide meridionally (Fig. 57), the cell $d^{6.6}$ unequally, the others equally. The dorsal cell divides equatorially and unequally. Diagram III. shows the ectodermal part of this quadrant at the end of the sixth cleavage. The actual condition in the egg at this period is shown in Figure 58, and at a slightly earlier stage in Figure 57.

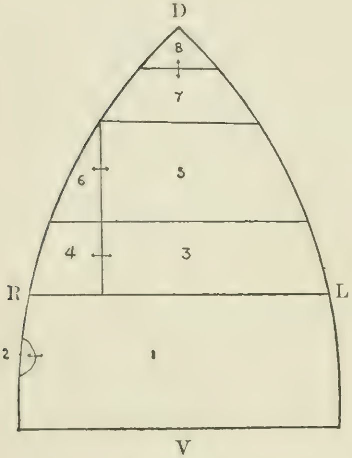

DIAGRAM II.

Diagram of quadrant *D* in the sixth generation. Only the second exponent designating the cells appears in the diagram, the first being in all cases 6.

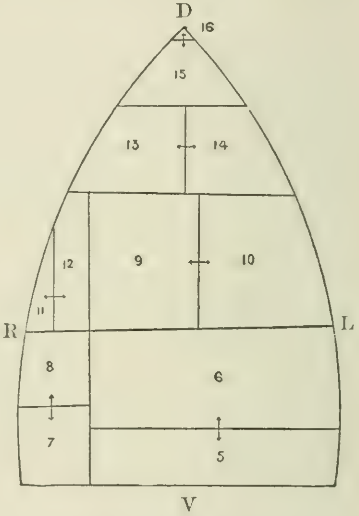

DIAGRAM III.

Quadrant *D* in the seventh generation. Only the second exponent is expressed, the first being in all cases 7.

The arrows connect cells of common origin, and show the direction of the spindles at the preceding division. R signifies right; L, left; D, dorsal; V, ventral.

Comparison of Diagram III. with the type diagram for the other three quadrants given on page 41, shows that the *directions* of the cell walls are the same in both, the inequality in the size of the cell in the quadrant D being the only difference.

In the *seventh cleavage*, the spindle appears first in the cell $d^{7.6}$, as shown in Figure 58, and the cell is divided meridionally into two equal cells, $d^{8.11}$ and $d^{8.12}$. The finished division is shown in Plate **8**, Figs. 66, 67, and 68. The plane separating these two cells is the median dorso-ventral plane of the embryo, as will be shown later.

Shortly after this division is completed, spindles appear in $d^{7.5}$, $d^{7.9}$, $d^{7.10}$, $d^{7.13}$, and $d^{7.14}$, as shown in Figure 66. In $d^{7.5}$ the spindle is dorso-ventral, hence lying in the shorter axis of the cell; the cell extends and divides into two equal dorsal and ventral parts, $d^{8.9}$ and $d^{8.10}$ (Figs. 67 and 68). The greater surface extension of $d^{8.9}$ in Figure 67 is due to its being spread out in a thin layer over the surface of the entoderm cell.

In $d^{7.9}$ and $d^{7.10}$ (Fig. 66) the spindles are also dorso-ventral in position, and the cells divide equatorially into equal parts, $d^{8.17}$, $d^{8.18}$, $d^{8.19}$, and $d^{8.20}$ (Figs. 67 and 68).

In $d^{7.13}$ and $d^{7.14}$ the spindles lie at right angles to those just described, and the cells divide meridionally and equally, forming $d^{8.25}$, $d^{8.26}$, $d^{8.27}$, and $d^{8.28}$.

Figure 67 is a view of this region after these cleavages are finished. As shown in this figure, a certain amount of shifting has taken place during cleavage, by which the cell $d^{7.7}$ has been excluded from its share in the boundary of the blastopore. As the cells divide, they withdraw their interior parts and extend in the direction of the spindle, as has been minutely described for other cleavages; in this way the dorso-ventral extent of quadrant D has been greatly increased. As a result the blastopore has been nearly closed (Fig. 63), and at the opposite end the animal pole has been pushed beyond the micromere end of the egg to its anterior side (Fig. 65).

Thus far the six larger left hand cells have divided, leaving six smaller cells (at the right and at the dorsal pole) undivided (Fig. 67).

Next, as shown in this figure, the cells $d^{7.7}$ and $d^{7.8}$ form spindles and divide. Each cleaves in the same manner as its larger companion cell has done, $d^{7.7}$ equatorially, $d^{7.8}$ meridionally. The products, $d^{8.13}$, $d^{8.14}$, $d^{8.15}$, and $d^{8.16}$, are shown in Figure 68 (compare Diagram IV.).

Next $d^{7.12}$ cleaves equatorially, like its companion cells $d^{7.9}$ and $d^{7.10}$. In $d^{7.12}$ the division is unequal, the ventral product, $d^{8.23}$, being much the smaller (Fig. 68).

The cleavage of $d^{7.11}$ occurs much later, and is likewise equatorial. I have not thought it necessary to introduce a special figure to show the cleavage of this minute cell.

In $d^{7.15}$ the cleavage also takes place late; it is meridional and equal. The resulting cells, $d^{8.29}$ and $d^{8.30}$, are shown in Figure 72 (Plate **9**). The minute dorsal cell $d^{7.16}$ does not divide.

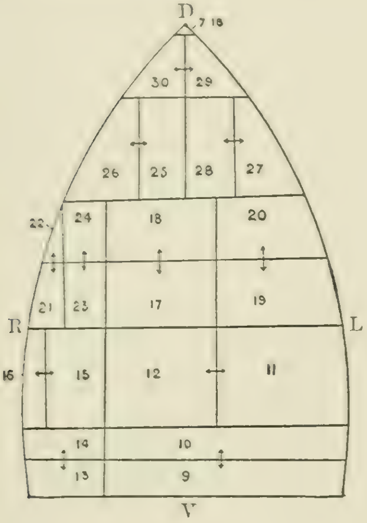

Diagram IV.

Quadrant D in the eighth generation, — except the dorsal cell, $d^{7.16}$, which does not divide farther. In the other cells only the second exponent is expressed, the first being in all cases 8. The arrows connect cells of common origin, and show the direction of the spindles at the preceding cleavage.

R signifies right; L, left; D, dorsal; V, ventral.

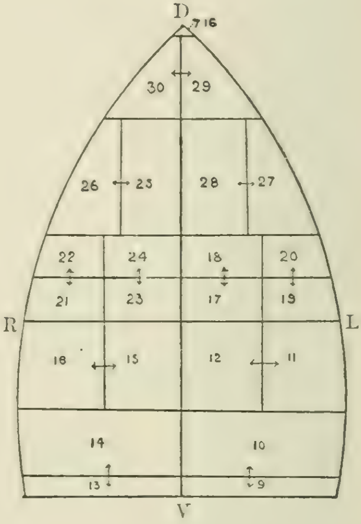

Diagram V.

Diagram of quadrant A, B, or C, in the eighth generation. Only the second exponent of the cells appears in the diagram, the first being 8. The small dorsal cell, $(a, b, \text{or } c)^{7.16}$, does not divide, remaining thus in the seventh generation. The arrows connect cells of common origin, and show the direction of the spindle at the preceding division.

R signifies right; L, left; D, dorsal; V, ventral.

There are thus 23 cells in the ectodermal part of the quadrant D at the end of the seventh cleavage. A diagram of this stage is annexed (Diagram IV.). Nearly this stage is represented in Figure 68.

(2) *The Quadrants A, B, and C.* — Owing to the regularity in the size of the cells in these quadrants, and the fact that they are purely ectodermal, the conditions observed are fairly simple as compared with

those in quadrant *D*. Figure 61 (Plate **7**) shows the anterior surface of the egg at the end of the sixth cleavage, and a diagram of a single quadrant at this stage was given on page 41. Comparing either the figure or the diagram with the scheme (Diagram III.) given on page 46 for the quadrant *D* at the same stage, the arrangement is seen to be the same except in two respects. (1) The cells belonging to the same lateral series are equal in *A*, *B*, and *C*, unequal in *D*. (2) Four ventral ectodermal cells additional are present in each of the quadrants *A*, *B*, and *C*; these are represented in *D* by the cells which have passed inward to form the entoderm.

As shown by the spindles in Figure 61, the first cells to divide are $a^{7.13}-c^{7.13}$ and $a^{7.14}-c^{7.14}$. The cleavage is meridional and equal. The resulting cells are $a^{8.25}-c^{8.25}$, $a^{8.26}-c^{8.26}$, $a^{8.27}-c^{8.27}$, and $a^{8.28}-c^{8.28}$. They are shown in Figures 72 and 75 (Plate **9**). (Compare Diagram V.)

Next follows the division of the six cells, $a^{7.6}-c^{7.6}$ and $a^{7.8}-c^{7.8}$, which together form part of a transverse girdle, surrounding the egg. The cleavage is meridional and equal. The resulting 12 cells, $a^{8.11}-c^{8.11}$, $a^{8.12}-c^{8.12}$, $a^{8.15}-c^{8.15}$, and $a^{8.16}-c^{8.16}$, forming as before a transverse girdle, are shown in Plate **8**, Figs. 69 and 70, and Plate **9**, Fig. 71.

Next ensues the cleavage of the transverse row containing the six cells, $a^{7.5}-c^{7.5}$ and $a^{7.7}-c^{7.7}$. These cells, as shown in Figure 61 (Plate **7**), are much flattened dorso-ventrally, and are of exactly the same form as the cells last discussed, which lie immediately dorsad of them. Moreover, each cell in this row corresponds in origin to a cell of the row last described, the two rows having been derived from the equatorial division of a previously existing transverse row, as shown in Figure 55. If mechanical conditions are decisive in determining the direction of the cleavage, these two rows should cleave in the same manner, i. e. both meridionally. Nevertheless, as shown in Figure 69 (Plate **8**), while the dorsal of the two rows divides meridionally, the cells of this ventral row all cleave equatorially. The axis of the cell in which the spindle lies is about half as long as the axis which is at right angles to it. The cells elongate in the direction of the spindles, and a very unequal division ensues. The ventral products are minute, while the dorsal ones are nearly equal in size to the mother cells. Figure 75 (Plate **9**) shows the anterior surface of the egg after this cleavage. The twelve cells produced are $a^{8.9}-c^{8.9}$, $a^{8.10}-c^{8.10}$, $a^{8.13}-c^{8.13}$, and $a^{8.14}-c^{8.14}$.

The division of the band of twelve small cells composed of $a^{7.9}-c^{7.9}$, $a^{7.10}-c^{7.10}$, $a^{7.11}-c^{7.11}$, and $a^{7.12}-c^{7.12}$, and shown in Figure 61 (Plate **7**), follows somewhat later. The cleavage is equatorial and the spindles lie in the short axes of the cells, as shown in Figure 75 (Plate 9). Just before division the cells elongate until the axis in which the spindle lies is longest, as shown in the cell $b^{7.12}$ of the figure last mentioned.

The cells $a^{7.15}-c^{7.15}$, near the animal pole, cleave meridionally. The spindle in $a^{7.15}$, and the cells $b^{8.29}$ and $c^{8.29}$, $b^{8.30}$ and $c^{8.30}$, are shown in Figure 72 (Plate 9). The minute cells $a^{7.16}-c^{7.16}$, like $d^{7.16}$, do not cleave further. The arrangement at the animal pole is now very irregular, and owing to this fact and the minuteness of the cells produced at the last cleavages it is very difficult to be certain of the exact origin of any given cell, though the origin of the *group* cannot of course be doubtful.

We have now accounted for all the cells of these quadrants except the four ventral cells of each quadrant, $a^{7.1}-c^{7.1}$, $a^{7.2}-c^{7.2}$, $a^{7.3}-c^{7.3}$, and $a^{7.4}-c^{7.4}$. These correspond in origin to the entoderm cells of quadrant *D*, and they do not cleave further until they are partly or entirely enclosed within the embryo, as will be shown later.

A diagram of that part of any one of the quadrants *A*, *B*, and *C* corresponding to the ectodermal part of quadrant *D*, and showing the conditions at the end of the seventh cleavage, is given on page 48 (Diagram V.). A comparison of this diagram with that for the corresponding stage of the quadrant *D* (Diagram IV. on the same page) shows that the direction of the cleavage planes, and hence of the spindles, is the same throughout in all cells of corresponding position, though there are many differences as to the equality or inequality of the cleavage products.

The general facts which may be deduced from the foregoing study of the seventh cleavage in the ectodermal parts of the egg are similar to those drawn from a study of the sixth cleavage, page 41.

(1) Every cell of any *quadrant* divides with its spindle in the same direction as the corresponding cell of any other quadrant.

(2) All the cells in any *layer* cleave with spindles in the same direction (in spite of great differences in the *form* of the cells.)

(3) No general law can be deduced as to the equality or inequality of the divisions.

(4) There is a tendency for the largest cells to cleave fastest. Certain very small cells (at the dorsal pole) do not cleave at all.

Other Changes during the Seventh Cleavage. — In almost every cleavage which has taken place, whenever the division was equatorial, — the spindles taking a dorso-ventral position, — it will have been noticed that the axis in which the spindle was formed was the short axis of the cell. On the other hand, the cells in which meridional cleavages have taken place have commonly been already somewhat elongated in the direction of the spindle. Therefore, at the occurrence of division, the short cells, cleaving equatorially, have changed form greatly, becoming more elongated dorso-ventrally, while the cells which cleave meridionally have already been of sufficient length to permit of the extension of the spindle without much change of form. As a result, there has been a great extension of the ectoderm dorso-ventrally. This produces first a complete closure of the blastopore. (Compare Figure 65, Plate **8**, with Figure 76, Plate **9**.) A second result, due to the larger size of the cells of the quadrant *D*, and perhaps partly also to the fact that they cleave first, is the further displacement of the animal pole of the egg from the micromere end toward the anterior side (Plate **8**, Fig. 65, Plate **9**, Fig. 76).

The closure of the blastopore is not sufficient to provide for the dorso-ventral extension brought about during the cleavage, so that, as a *third* consequence, the cells at the ventral pole of the egg, where the blastopore was previously situated, are pushed over or under one another, the ectoderm tending to become two-layered in this region. A comparison of Figure 63 (Plate **8**) with Figure 73 (Plate **9**) shows the resulting conditions. In the latter figure the entoderm ($d^{8.1}$ in Fig. 63) is entirely enclosed, and the ventral cells $a^{7.1}-c^{7.1}$, $a^{7.2}-c^{7.2}$, $a^{7.3}-c^{7.3}$, and $a^{7.4}-c^{7.4}$ have become crushed together, and several of them, as $a^{7.2}$ and $b^{7.3}$, are almost hidden by surrounding cells. The beginning of the two-layer condition is shown in frontal section in Figure 80 (Plate **10**), from the same egg as that shown in Figure 73 (Plate **9**).

Meanwhile other cleavages are taking place in quadrant *D*, leading to still further modifications of the structure of the egg. It is therefore necessary to return to a consideration of this quadrant.

Quadrant D. — By reference to the diagram of the cells of this quadrant at the end of the seventh cleavage (Diagram IV., page 48), it will be seen that there are now present, exclusive of the entoderm, twenty-three cells, arranged somewhat irregularly. Approximately the same stage, as it actually appears, is shown in Figure 68 (Plate **8**).

In this egg spindles have appeared in the large cells $d^{8.11}$ and $d^{8.12}$, and later they each become divided into two equal cells. It is worthy of notice that the two spindles are not parallel, but make a slight angle with each other. The two cells lie on opposite sides of the median dorso-ventral plane, so that the angle between the spindles indicates the beginning of a tendency to *bilateral* cleavage. The inclined position of the other spindles (in $c^{7.7}$ and $c^{7.11}$) is indicative of the same fact. The tendency toward bilaterality is apparently due to the crowding of the cells from all directions toward the blastoporic region, which lies at the ventral border of $d^{8.9}$ (Fig. 68). The cells resulting from the division of $d^{8.11}$ and $d^{8.12}$ are $d^{9.21}$, $d^{9.22}$, $d^{9.23}$, and $d^{9.24}$; they are shown in Figure 74 (Plate **9**).

Next the four cells immediately dorsad of these, $d^{8.17}$, $d^{8.18}$, $d^{8.19}$, and $d^{8.20}$, develop spindles in their short axes (Plate **8**, Fig. 68), which as a result of extension become the long axes (Fig. 74, Plate **9**), — the cleavage being in each case equatorial and equal.

Now the four large cells $d^{8.25}$, $d^{8.26}$, $d^{8.27}$ and $d^{8.28}$, shown in the dorsal part of Figure 68 (Plate **8**), cleave equatorially also.

As a result of these many equatorial cleavages the quadrant *D* becomes greatly increased in dorso-ventral extent. The animal pole is forced farther upon the anterior side of the egg, toward the blastopore, so that the cells of the quadrant *D* come to occupy in the region of a sagittal section much more than half the circumference of the egg (Plate **9**, Fig. 76).

The two ventral cells $d^{8.9}$ and $d^{8.10}$ meanwhile divide meridionally, completing the separation of quadrant *D* into two portions lying on each side of the median line (Fig. 74). However, the egg is not yet completely separated by cleavage planes into right and left halves, for the entodermic cell $d^{9.4}$ occupies the median plane at even a later stage than this (Plate **10**, Fig. 83).

This is the latest stage to which I have traced the cleavage in the ectodermal part of quadrant *D*. Diagram VI. shows the condition at this time.

The dorso-ventral extension of the ectoderm, and consequent crowding together of the cells in the region of the blastopore, are still further increased by the eighth cleavage of the large cells $a^{8.25}-c^{8.25}$, $a^{8.26}-c^{8.26}$, $a^{8.27}-c^{8.27}$. and $a^{8.28}-c^{8.28}$, belonging to the other quadrants, which likewise divide equatorially and equally (Plate **9**, Fig. 75).

The blastoporic region has now become distinctly two-layered, as shown in Figure 77. The cells of quadrants *A*, *B*, and *C* are turned in and pushed dorsad, in the same manner as happened in early stages to the large ventral cell of quadrant *D*. The anterior lip of the blastopore thus becomes two layers thick, while the posterior lip is formed of a single layer of cells from the quadrant *D*, resting against the entoderm cells. Between these ventral cells of quadrant *D* and the infolding cells of the other quadrants, a slight notch appears, marking the position of the blastopore. (At an earlier stage the blastopore was entirely closed, as shown in Figure 73.) The blastopore notch lies, not directly at the macromere end of the egg, but at some distance on the posterior side of it.

As the cells of the anterior lip of the blastopore are turned inward, some of them begin to divide. Spindles in these cells are shown in Plate **9**, Figs. 75 and 77. The form and position of the cells have changed so much at this time that it is impossible to determine with certainty whether the cleavage should be considered equatorial or meridional. In the cases figured the spindles are nearly or quite transverse, so that in some of the cells the division is meridional.

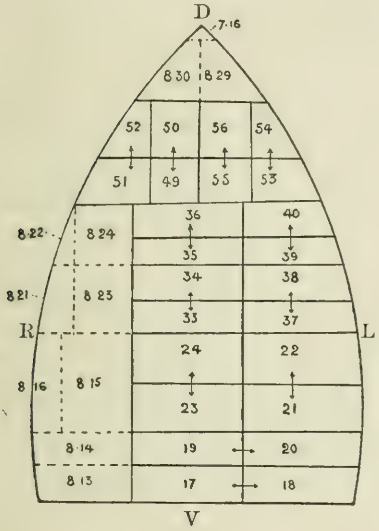

Diagram VI.

Diagram of quadrant *D* at a time when most of the cells have passed into the ninth generation. All cells in the ninth generation are bounded by continuous lines, and are designated by the second exponent belonging to the cell, the first exponent being in each case 9. In the other cells both exponents are given. The arrows connect cells of common origin, and show the direction of the spindle at the last division.

R signifies right; L, left; D, dorsal; V, ventral.

The cleavage of the ectoderm has now been traced to the eighth generation in all parts of the egg, and in the greater part of the quadrant *D* to the ninth generation.

With this ends the account of the cleavage of the ectodermal cells. The small size and the great displacements of the blastomeres, especially in the regions of the blastopore and the animal pole, render it impossible to determine with certainty their identity in later stages, and the real direction of cleavage is masked by crowding and deformation of the cells. It would perhaps be of little interest in connection with the laws of cleavage to carry the study further, as it is scarcely to be presumed that the later divisions would exhibit any phenomena differing fundamentally in kind from those already shown in the earlier stages.

We must now turn to a consideration of

The Entoderm.

The cells which I have called the entoderm — following in this Zelinka ('91) and Tessin ('86) — are those derived from the single large cell of the quadrant *D*, which passes within the egg in the manner already described. I have already given an account of the first cleavages of this cell after it has become partially covered by the other blastomeres. As will be recalled, at the fifth and sixth cleavages the spindles occupied twice in succession the same position, one end lying in the anterior median line, between the ventral cells of quadrants *A* and *B* (Plate **5**, Fig. 35, and Plate **6**, Fig. 48). Here was given off at each of these cleavages a minute vesicle, the entire process being comparable in external features to the successive formation of two polar cells at a given spot on the surface of the egg. The two vesicles thus formed maintain their position for some time (Plate **7**, Fig. 55), but as the surrounding cells become invaginated, I have found it impossible to follow their later fate.

We will follow the cleavage of the large cell $d^{7.1}$ (Plate **6**, Fig. 50), which forms the greater bulk of the entoderm.

After the sixth cleavage (Fig. 49), the asters in $d^{7.1}$ at once separate nearly in the dorso-ventral axis of the egg, as shown in Figure 50. The line joining them is at first a little oblique, the ventral aster being a little to the right. This obliquity soon corrects itself, and the asters come to lie in the sagittal plane. As the spindle is formed, its dorsal end moves to the posterior side, so that the spindle is no longer in the dorso-ventral axis of the egg. This stage is shown in Figure 64 (Plate **8**); as may be observed in this figure, the spindle is neither in the longer axis of the cell nor at right angles to it, but oblique. The cloud of granules, which soon after the last division occupied a region on the anterior side of the cell, underneath the two vesicles $d^{6.2}$ and $d^{7.2}$, now surrounds the aster at the dorso-posterior end of the spindle.

The cleavage is unequal, separating (Fig. 65) a smaller dorso-posterior cell, $d^{8.2}$, from a larger anterior one, $d^{8.1}$. The cloud of granules remains in the smaller, dorsal cell, forming a band about its periphery, so as to leave a free space surrounding the nucleus. The position of the animal pole of the egg with reference to this cell should be carefully noted, as the relation remains constant, at least for a time, during the considerable shiftings which take place. As seen in Figure 65, the animal pole lies at the anterior margin of the cell $d^{8.2}$.

Before the *eighth cleavage* takes place, the blastopore has become closed and its anterior margin has begun to pass into the two-layer condition, as previously described. The larger cell, $d^{8.1}$, divides before its mate, by a spindle at right angles to the previous spindle. The cleavage is equal, forming the two large right and left cells $d^{9.1}$ and $d^{9.2}$, shown in Plate **10**, Fig. 80. The plane separating these cells coincides with that separating the quadrants A and B on the anterior side of the egg, and also with that separating the two cells $d^{8.11}$ and $d^{8.12}$ on the posterior side (Plate **8**, Fig. 68). As this plane also passes through the animal pole and the blastopore, it divides the egg into symmetrical halves, and is the median dorso-ventral or sagittal plane of the embryo.

Later the small cell, $d^{8.2}$, develops a spindle in the same direction as the spindle of the seventh cleavage, in the shorter axis of the cell, and divides into two very unequal cells. The anterior or ventral cell, $d^{9.3}$, is a minute vesicle, whereas the dorsal or posterior blastomere, $d^{9.4}$, is scarcely smaller than the mother cell. The process of budding off this small cell is shown in Plate **10**, Figure 80. The vesicle lies between the two large cells $d^{9.1}$ and $d^{9.2}$, and, like the minute cells $d^{6.2}$ and $d^{7.2}$, can be traced but a short distance, soon becoming lost among the many cells by which it is surrounded.

In the *ninth cleavage*, spindles are formed in the cells $d^{9.1}$ and $d^{9.2}$ in the position foreshadowed by the asters in Figure 80, — that is, antero-posterior, and at right angles to the preceding spindles, — and the cells divide equally, forming the four cells $d^{10.1}$, $d^{10.2}$, $d^{10.3}$. and $d^{10.4}$. Figures 76 and 81 show the entoderm at the close of these divisions — the nuclei of the cells in question being still connected in pairs by interzonal filaments. The blastopore is now present as a distinct notch; its anterior or dorsal lip has become two-layered, owing to the folding inward of the cells of the anterior quadrants. The animal pole (*pol. anm.*, Fig. 76) has moved a considerable distance on to the previously anterior surface, lying still at the anterior margin of the entoderm cell $d^{9.4}$. As the side view (Fig. 76) shows, a frontal plane carried through the long axis of the egg at this stage would cut the nuclei of all the entoderm cells, as realized in the frontal section, Figure 81 (Plate **10**).

As soon as the cells, after the cleavage process is entirely finished, have lost their strong tendency to maintain a form as nearly spherical as possible, a sudden and considerable change of relative position takes place. The four entodermal cells, $d^{10.1}-d^{10.4}$ become much flattened dorso-ventrally, and the invagination of cells at the anterior lip of the blastopore increases in extent. These cells press most strongly upon the anterior surface of the ventral entodermal cells, forcing them toward the posterior side. An early stage in the process is shown in Plate **9**, Figure 77. Two of the cells of the invaginating ectoderm have flattened themselves against the entoderm cells in such a way as to form a direct continuation of the longitudinal series of interior cells. This longitudinal series is however tending to become curved by the displacement of the cell $d^{9.4}$ in a dorsal and anterior direction. This cell, together with the animal pole, has moved a very slight distance toward the macromere end of the egg. The animal pole now lies (Fig. 78) directly above the plane separating the cells $d^{10.1}$ and $d^{10.3}$ from $d^{10.2}$ and $d^{10.4}$, instead of above the posterior margin of the cells $d^{10.2}$ and $d^{10.4}$, as previously. A frontal plane carried through the long axis of the egg would not now cut the cell $d^{9.4}$ at all. Figure 82 shows a view from the animal pole, the outer layer of ectoderm cells being supposed to be removed from the dorsal half of the egg, while the entoderm cells remain in position.

This process of *rotation* of the entodermic contents, as one might call the phenomenon, continues still farther. Figure 79 shows a stage in which the process is much more advanced. The ectodermal plug at the anterior lip of the blastopore has become very much thickened, and projects farther posteriad; the four large entoderm cells $d^{10.1}-d^{10.4}$, of which of course but one pair is shown in the side view, are now so displaced that the plane separating the pair, which previously lay in the short axis of the egg (Figs. 76 and 78), now lies in the long axis (Fig. 79). The line connecting the centres of a given lateral pair is now at right angles to the line previously connecting them.

At this time the five large cells constituting the entoderm — the minute cell $d^{9.3}$ not being traceable farther — begin to undergo karyokinetic changes preparatory to division. The spindles in various stages are seen in three of the cells in the side view, Figure 79; the same stage, slightly earlier, is shown from the animal pole in Figure 83 (Plate **10**), in which the covering ectoderm is supposed to have been removed from the dorsal side of the egg. As a comparison of Figures 79 and 83 shows, the spindles do not lie in parallel planes, so that no single view can give a complete representation of their positions. Nevertheless, Figure 83 shows that the arrangement is distinctly bilateral. The cell $d^{9.4}$ lies in the middle line, with its spindle in the sagittal plane of the egg; the spindles in the other cells all radiate outward from the region occupied by $d^{9.4}$, the sagittal plane passing through this cell forming a plane of symmetry for all. The median plane thus indicated coincides with that already defined by the line separating the quadrants A and B anteriorly, and the boundary between the cells $d^{8.11}$ and $d^{8.12}$ posteriorly; it passes through the animal pole and the blastopore.

This movement of the entodermal blastomeres is of course simply a continuation of the rotation inaugurated at the passage from the four- to the eight-cell stage. The ectodermic cells continually withdraw their deeper parts and increase their surface area at division; in this way cells are continually forced in at the blastopore. These press upon the anterior and ventral aspects of the entoderm cells, forcing them backward, as already described. The pressure is greatest in the median region, so that the anterior or ventral ends of the cells on the two sides of the median plane are forced apart, the axes of the cells become oblique to the long axis of the embryo, and the oblique position of spindles shown in Figure 83 results.

Beyond this point it is impossible to trace the development cell by cell. In Asplanchna there is a period, intervening between the stage to which it is possible to trace the cleavage step by step (about 120 cells) and the stage of recognizable differentiation of organs, during which the cells divide and become very minute. The cells probably reach the number of from 250 to 500, and the process of extension of cells and consequent "rotation" and invagination of parts of the embryo continues. A sagittal section of the embryo at about the time of the beginning of differentiation of organs is shown in Figure 84. It thus becomes impossible to trace the fate of individual blastomeres, or even, except in a most general way, the fate of the different regions of the embryo during the later portion of the cleaving. From the small size of the adult rotifer, I had hoped that it would prove to be a favorable object for an exact study of the cytogenetic history of organs; in Asplanchna this turns out not to be the case. But, on the other hand, for a study of the factors in the early developmental processes it has shown itself well fitted.

My study of the processes in the early development of Asplanchna therefore closes with the stages shown in Figures 79 and 83 (Plates **9** and **10**).

For critical comparison of my observations with those of Zelinka and other workers on the development of the Rotifera, the reader is referred to Part Second.

I shall now proceed to a discussion of the bearing of the foregoing observations upon the problems already proposed, as well as upon other related subjects.

III. Discussion of the Bearing of the Observations on the Problems.

In the following discussion I shall adopt in general the order pursued in my "Statement of Problems," taking up successively the various theories in regard to cleavage and gastrulation, and pointing out what bearing the observations above detailed have upon these theories. This will be followed by a *résumé* of the general conclusions which may be drawn from the work.

We will therefore first take up a discussion of the cleavage, and of the theories bearing upon it.

1. Cleavage.

A. The Direction of Cleavage.

(1) *Berthold's theory of surfaces of least area.* (See page 4.) — The two- and four-cell stages in Asplanchna agree well with the conditions demanded by the law of least surfaces. The peculiar arrangement of blastomeres in the four-cell stage, agreeing as it does with the four-cell stage of animals of the most various systematic positions, and with the four-cell stage of many plants, seems probably due to some very general law. In all these cases only three cells meet along one common line. As this is the arrangement demanded by the principle of least surfaces, the conclusion seems perhaps justifiable that this principle of least surfaces is that common law.

The eight-cell stage also fulfils the requirements of the principle of least surfaces. But from this stage onward, many of the conditions found are irreconcilable with the view that this principle is a determining factor. Six of the cells in the eight-cell stage divide in a manner that squarely defies the principle of least surfaces. Nor does the arrangement of cells in the resting periods agree better with the principle. As pointed out on page 30, the flat, almost disk-shaped form taken by the cells of quadrant *D* during the ten-cell stage (Figs. 23 and 25, Plate **3**) and the sixteen-cell stage (Figs. 31 and 32, Plate **4**) is widely at variance with the demands of the principle of least surfaces. The form of the cells in quadrants *A*, *B*, and *C* during their resting period in the sixteen-cell stage (Figs. 30 and 34) is equally impossible of explanation on the least surfaces theory. Many other cases could be adduced in which this principle is contradicted, but a fuller discussion of these cases will be given under the next theory (Hertwig's law). In general, any case which is not in agreement with Hertwig's law is likewise inexplicable by Berthold's principle, so that all the cases cited later as opposed to Hertwig's law can be utilized equally well against the principle of least surfaces as a determining force.

It should be noted that Berthold did not in any sense maintain that this principle is the *decisive* factor in cell division, or the arrangement of cells in tissues. He recognized that the conditions in a living cellular body are widely different from those in a simple vesiculated fluid, and that the conditions actually found in plant tissues are often inexplicable by the principle of least surfaces, — in many cases, indeed, directly opposed to it. "Aber nothwendig ist das in der Zelle nicht, wie bei den Flüssigkeitslamellen. Denn wir sahen schon früher, dass die Symmetrieverhältnisse der Zellen von der äusseren Form oft vollständig unabhängig werden, und auch unter Mitwirkung der äusseren Formverhältnisse können bei dem ineinandergreifen der verschiedenen Factoren sich Theilungsrichtungen ergeben, die mit den Forderungen des Princips der kleinsten Flächen nicht in Uebereinstimmung stehen." (Berthold, '86, p. 230.) Berthold ('86, p. 230, Taf. 4) describes and figures many cases in which the arrangement and division of cells is not in accordance with the principle of least surfaces.

The fact that a single cell may at one time take such a form as that which $d^{6.3}$ shows in the surface view in Figure 37 (Plate **5**), and in section in Figure 38, and at another time have the form exhibited by the same cell in Plate **7**, Figure 54 (surface), and Plate **6**, Figure 48 (section), while the shape of the egg remains unchanged, demonstrates that we are not here dealing with a problem of the statics of a vesiculated fluid; a single simple principle can no more account for the forms taken than it can for the protean changes of shape of an Amœba.

By this I of course do not mean to imply that it is not possible, and perhaps probable, that the laws of surface tension do, within certain limits, modify the form and arrangement of cells, as maintained and discussed at length by Berthold. Wherever the arrangement demanded by the principle of least surfaces is not in conflict with other purposes of the organism, or, to put it upon a less teleological basis, where it is not in conflict with stronger influences than the force of surface tension, the cells probably accommodate themselves to the demands of that principle. The point of importance, however, is that this is not a *decisive* factor, but may at once be overcome when other influences in the organism antagonize it.

Zimmerman ('93) holds that the general arrangement of cells in accordance with the principle of least surfaces in plant tissues is not due to surface tension at all, but to turgor. Turgor, however, can hardly be a factor in the cleavage of the egg, where no increase in size is taking place.

(2) *Hertwig's law of the spindle in the longest axis of the protoplasmic mass.* (Compare page 5.) — This is, so far as I know, the only principle for which the claim is made, that it is *the* decisive factor in determining the direction of the spindle. The statement quoted above (page 5) is from Hertwig's general text-book on the subject, in which it is presumable that care would be taken not to mislead the reader unacquainted with the literature into taking a special phenomenon for a law of general import. On the same page it is stated that "Mit diesen Regeln stimmen die Erscheinungen, wie sie bei der Zelltheilung und insbesondere bei der Eifurchung beobachtet werden, fast ausnahmslos überein." (Hertwig, '93, p. 175.) The "law" has been accepted by others in the same general bearing. Thus Ziegler ('94, p. 154) questions the validity of cases apparently not in agreement with the rule, holding that they are due either to inexact study (cylindrical epithelium), or to the difficulties of determining in the presence of a mass of yolk (amphibian egg) which *is* the longest dimension of the protoplasmic mass. This principle has become the most widely known and generally accepted of any of the principles which have been proposed in regard to the determining factors in cell division. I shall therefore discuss it at somewhat greater length than Berthold's principle, analyzing in detail the evidence on the subject from my own work, and reviewing that advanced by others.

A comparison of the very first cleavage of Asplanchna with that of Callidina (Zelinka, '91) shows that in the Rotifera the form of the egg is not the factor determining the position of the first cleavage spindle. For in the two forms the first cleavage spindle bears the *same* relation to the animal pole, or place of polar-cell formation, but a *different* relation to the long axis of the egg. In Asplanchna the spindle at the time of division lies in the long axis of the egg (though a little earlier it is oblique), whereas in Callidina (Zelinka, '91, Taf. I. Fig. 5) the spindle at division is oblique to both the longer and shorter axes, — the place of polar-cell formation not being the same as in Asplanchna, but much nearer one end of the egg. The orientation of the spindle in these two rotifers, then, is constant with reference to the animal pole, but variable with reference to the form of the egg.

The passage from the eight- to the sixteen-cell stage in Asplanchna is particularly instructive. The asters of the six cells of quadrants *A*, *B*, and *C* first separate in such a way that the line joining them lies in the long axis of the cell (Plate **3**, Fig. 17), then a rotation takes place (Fig. 18) by which the line joining the asters, i. e. the axis of the future spindle, is brought into the shortest axis of the cell (Figs. 19–24). The six spindles are then formed in the shortest axes of the cells (Figs. 20–28), and the *planes* of cleavage accordingly coincide with the long axes of the cells.

The simple fact that there are divisions in which the spindles lie in the shortest axis of the cells is of course a direct contradiction of Hertwig's law. The case becomes even more striking, however, when the movements of the asters are taken into consideration. They *at first* lie in the position demanded by the law, but *move from* this position to that which directly contradicts the law. (See pages 25, 26.)

Hertwig ('93, p. 175) has cited a similar phenomenon, described by Auerbach, as proof of his law. Auerbach ('74) observed in the eggs of Ascaris nigrovenosa, at the time of fertilization, that the two pronuclei often come together in such a way that the plane separating them lies in the short axis of the egg. Since the axis of the first cleavage spindle commonly coincides with the plane separating the pronuclei, the result in the eggs of this species of Ascaris would be that the spindle would occupy the short axis of the egg. But the two pronuclei after meeting undergo a rotation through an angle of 90 degrees, thus bringing the spindle into the *long* axis of the egg. Ziegler has recently observed with even greater clearness the same phenomenon in the eggs and cleavage cells of other nematodes (Ziegler, '95, Taf. XVIII. Figs. 40–42), and in the eggs of echinoderms ('94). He observed in nematodes in some cases that the line joining the two asters on opposite sides of the nucleus lies in the short axis of the egg, and that then follows a rotation of the whole complex, till the line joining the asters — the axis of the forming spindle — occupies the longest axis of the egg. Ziegler, like Hertwig, has interpreted this change of position as a confirmation of Hertwig's law, and the interpretation is certainly the most natural and apparently well grounded that could be given.

Nevertheless we have in Asplanchna an entirely similar phenomenon, but occurring under such circumstances as to give a direct contradiction, instead of a confirmation, of Hertwig's law.

It is instructive also to notice that in the eight-cell stage of Asplanchna, notwithstanding the great variety in the form of the cells, the direction of the cleavage spindles is the same in all the cells. Thus $d^{4.1}$ (Plate **2**, Fig. 15), though irregular in shape, is of such a form that it is possible to be confident that the spindle does lie in the greatest dimension of the cell. The blastomere $d^{4.2}$ (Plate **2**, Figs. 14 and 16) is so exceedingly irregular in form, that it is impossible to determine with certainty which is the longest axis. The cells $a^{4.2}-c^{4.2}$ are irregularly triangular, and the direction in which the spindle lies is the shortest line connecting any apex with the middle of the opposite side (Plate **3**, Figs. 18, 19). Finally, the cells $a^{4.1}-c^{4.1}$ are approximately rectangular in form, with one of the axes much longer than the other; the spindles lie in the shorter axes (Figs. 20–22). In every case the spindle, whatever the form of the cell, lies in a meridian connecting the animal pole with the vegetative pole of the egg. The only rational conclusion from this fact is, that the position of the spindles is determined by some factor unconnected with the form of the cells.

The theory that the direction of the spindles is due to their taking a position of *equilibrium* determined by the mutual attraction of spindle and protoplasm, so strongly insisted upon by Ziegler ('94, p. 140), is likewise inconsistent with the movements of the asters in the eight-cell stage of Asplanchna. Ziegler holds that, since the greater mass of protoplasm must exercise the greater attraction, the spindle in the short axis of the cell is in a position of unstable equilibrium; if by any cause it is moved in the slightest degree to one side or the other, it must inevitably swing into the long axis of the cell, where alone it can be in a position of stable equilibrium. This he holds to be the explanation of the movements of asters and nuclei observed by Auerbach in nematodes, and by himself in nematodes and echinoderms, as mentioned above. An oblique position of asters and nuclei, such as is shown in the cell $a^{4.1}$, Figure 22 (Plate **3**), is intelligible on this assumption if the movement taking place is from the shorter toward the longer axis. But in this cell, as in the other five of the quadrants *A*, *B*, and *C* at this stage, the movement is from the longer axis toward the shorter. The hypothesis that the movement is due to simple attraction between the protoplasm and the fundament of the spindle, varying with the *mass* of the protoplasm, is totally inconsistent with such a notion.

The passage from eight to sixteen cells is not the only cleavage in Asplanchna which is irreconcilable with Hertwig's principle. At the transition from the sixteen-cell to the thirty-two-cell stage, there is a similar regularity in the position of the spindles coincident with variety in the form of the cells. The four dorsal cells $a^{5.4}-d^{5.4}$ divide equatorially, three of them with spindles in the longer axis; one, $d^{5.4}$, with the spindle in the shorter axis (Plate **4**, Fig. 33).

Again, in the sixth cleavage the cell $d^{6.3}$ shows the same phenomenon of rotation of the spindle into the shorter axis of the cell (Plate **5**, Fig. 37, Plate **6**, Fig. 46, and Plate **7**, Figs. 53 and 54). There is the same regularity in the direction of cleavage as noticed in the preceding cleavages, although there is variation in the form of the cells. Thus, $d^{6.4}$, the companion cell of $d^{6.3}$, whose division with spindle in the short axis has just been cited, cleaves with the spindle parallel with that in $d^{6.3}$, but owing to the form of the cell the spindle in $d^{6.4}$ occupies the long axis (Plate **7**, Fig. 57, cleavage finished). The cells of the ventral layer (Plate **6**, Fig. 47) divide with spindles in the same direction as those in the cells of the second layer, although in the one layer the spindles must thereby occupy the short axes of the cells, in the other the longer axes.

In the seventh cleavage a still more striking case occurs. The middle of the embryo is surrounded by two rows of eight cells each, of precisely the same form and size, the dorsal row composed of the blastomeres $a^{7.6} - d^{7.6}$ and $a^{7.8} - d^{7.8}$, the ventral row of $a^{7.5} - d^{7.5}$ and $a^{7.7} - d^{7.7}$. These two rows are shown in Figure 61 (Plate **7**), for the quadrants *A*, *B*, and *C*, and in Figure 57 for the quadrant *D*. In both rows, every cell but one in each row ($d^{7.7}$ and $d^{7.8}$, Fig. 57) is strongly flattened dorso-ventrally, so that the lateral extent of the cell is much greater than the dorso-ventral extent. If the form of the cell determines in any way the direction of the spindle, it is certainly to be anticipated that the direction of cleavage will be the same for the cells of both rows. On the contrary, *all the cells of the dorsal row divide meridionally*, while *all the cells of the ventral row divide equatorially.* In every cell of the dorsal row, except possibly $d^{7.8}$, the spindle lies in the *long* axis of the cell; in every cell of the ventral row, except $d^{7.7}$, the spindle lies in the *short* axis of the cell. The exception of a single cell in each row gives a finishing touch to the proof that the form of the cells is not the factor determining the direction of cleavage. The fact that the cell $d^{7.8}$ divides with its spindle in the same direction as the spindles of all the cells in the same row, but not, as in the other cells, in the long axis of the cell, while $d^{7.7}$ likewise divides with its spindle in the same direction as those of the other cells of *its* row, but not, like them, in the short axis, demonstrates that the dorsal row is not so constituted that all the spindles must take their positions in the long axis, nor the ventral row so that all must take their positions in the short axis. It demonstrates, in other words, that the relative dimensions of the different axes of the cells does not determine the direction of the spindles in either one way or the other. (The cleavage of these two series of cells is shown for the quadrants *A*, *B*, and *C* in Plate **8**, Figs. 69 and 70; in $d^{7.6}$ in Plate **7**, Fig. 58; in $d^{7.5}$ in Plate **8**, Fig. 66; in $d^{7.7}$ and $d^{7.8}$, in Fig. 67.)

Still other divisions in which the spindle lies in the short axis have been followed out in the descriptive portion of this paper.

We must conclude, therefore, that a very large number of cell divisions in the cleavage of Asplanchna directly contradict Hertwig's law that the spindle during division comes to lie in such a position that its axis coincides with the greatest axis of the protoplasmic mass. The characteristic feature of the cleavage is *regularity* in the direction of the spindles, coupled with great *variation* in the form of the cells, thus excluding any close relation between these phenomena.

What is the evidence upon which this law has been based?

It is chiefly experimental, though there is likewise a certain amount of evidence based upon the observation of normal cleavage.

Let us consider first the evidence derived from experiment. The experimental studies of Pflüger ('84), Roux ('85), Driesch ('92), Hertwig ('93^a), Born ('93 and '94), Ryder ('93), and Ziegler ('94), on the effects of pressure upon the direction of the spindle, are so well known that it is not necessary to review them in detail. It is sufficient to state the general result. With rare exceptions it has been found that when the egg or the cleavage cell is so modified in form that one of the axes which may be passed through its protoplasmic mass is distinctly greater than the others, the spindle at cleavage comes to lie in this axis. I do not propose to enter upon an analysis of these experiments, nor to attempt to explain in any different manner the results gained. A study of the works of the authors above cited, and a repetition of the pressure experiments upon the eggs of the toad (Bufo lentiginosus Shaw) during the spring of 1895, have convinced me that the explanation commonly given is the one most in agreement with the conditions, and, from the evidence, most probably correct, *for these cases*. But whatever we may hold as to the validity of the explanation for these cases, we know that the principle upon which it is based cannot be *generalized*, since in many other cases it is directly contradicted by the facts. Before suggesting how the experimental results may perhaps be reconciled with the apparently contradictory phenomena observed in other cases, it will be necessary to consider the evidence gained by other means, as well as such experimental evidence as is *against* the principle.

First, then, we have the fact that the experimental evidence itself is not concordant upon this point. Roux ('85) found that under certain circumstances in deformed frogs' eggs the first cleavage plane sometimes, though rarely (Roux, '94[a], p. 274), passed through the greater axis of the cell, the spindle therefore lying in the shorter axis. Eycleshymer ('95) experimented as to the effects of pressure on the eggs of Amblystoma tigrinum, and found that when the eggs were compressed laterally to *one half* their normal equatorial diameter, there was little or no relation between the direction of cleavage planes and the greater or less dimensions of the egg. "The first vertical in the thirty-four eggs examined showed no constant relation to the compressed surfaces, in seven passing through the longest equatorial diameter; in nine through the shortest; in eighteen between the two." (Eycleshymer, '95, p. 353.) In experiments of a different nature, Morgan ('95) observed that the shaken eggs of Sphærechinus often divide at the first cleavage into three equal blastomeres, and in such cases at the *next* cleavage the three spindles lie in the short axes of the cells.

When we turn to the evidence from observation of normal cell division, there is the same disagreement that is met with in the experimental evidence. Until within a few years investigators in zoölogical lines have not paid attention to the exact relations of the spindle to the cell axes, so that little was to be found in the literature to emphasize the necessity of caution in accepting at once the generalizations from the first experimental results. In cases where cells containing spindles were figured, there was generally an apparent agreement with the principle that the spindles are in the long axis, but so long as it was not determined by observation whether this elongation of the cell was a *consequence* of the position of the spindle or a *cause* of it, the evidence was worthless, as pointed out by Heidenhain ('94), and as clearly illustrated in the preceding pages.

In botanical literature the case was somewhat different, and seven years before Hertwig ('93) had stated that the phenomena observed in cell division agreed "fast ausnahmslos" with his law, Berthold ('86, p. 230), in his thorough and comprehensive work on the subject, had said: "Sehr oft theilen sich prismatische oder cylindrische Zellen der Länge nach, wenn das Prinzip [of least surfaces] eine Querwand, der Quere nach, wenn es eine Längswand verlangte. So theilen sich oft die Markzellen, die Zellen der Grundparenchyms sich entwickelnder Blätter nur quer, *obwohl ihre Höhe im Vergleich zur Breite nur gering ist*" [Italics mine]. He had also given many examples of the conditions thus characterized.

Recently the attention of zoölogists has been directed to a careful observation of these relations, and a number of facts are now at hand which bear upon the subject.

Ziegler ('95) has studied the cleavage of certain nematodes (Diplogaster longicauda, Rhabdites teres, and Rhabditis nigrovenosa) with especial reference to the relations of cell form to the direction of cleavage, and finds that the conditions in these cases *confirm throughout the law of Hertwig.* In the normal cleavage the spindle always places itself in the long axis of the cell, even though a rotation of the nucleus and asters from their first position is often necessary to accomplish this result. And in cases where the egg is deformed by some outer agent, as pressure by the walls of the oviduct or the like, the normal position of the spindle is changed to agree with the changed form of the cells, the spindle lying in the long axis in every case. The agreement with Hertwig's law is complete.

On the other hand, zur Strassen ('95 and '96) has studied the cleavage of another nematode, Ascaris megalocephala, with the same questions in mind, and has come to *opposite* results. In the two-cell stage one cell divides with the spindle in the long axis, the other with the spindle in the short axis, and in later stages a similar independence of the position of the spindle and relative dimensions of the cell is shown. Zur Strassen ('95, p. 86) concludes: "Ich halte vielmehr den Kern für befähigt, vermöge ihm inhaerenter Eigenschaften eine gewollte Theilungsrichtung herbeizuführen, selbst wenn mechanische Hindernisse von nicht unbedeutender Höhe dem entgegenstehen."

Other observations bearing upon this question are much scattered. Cases are not uncommon in which authors have figured spindles in the shorter axes of the cells, but unless the observer's attention has been especially directed to the question, such figures are of little value, since a slight change in the position from which the cell is viewed produces a foreshortening which gives very different apparent relative dimensions to the axes. Heidenhain ('95, p. 553) gives a number of such cases, from most of which the evidence is weakened by this consideration. However, the case mentioned by Heidenhain of the germinal disk of the cephalopod egg as figured by Watase ('91) cannot be explained away upon this ground.

Some other instances may be mentioned.

In the formation of the "germ bands" in the Polychæt Amphitrite, according to Mead ('94, p. 467), "the axes of the spindles in these divisions lie in the shortest diameter of the cells, and apparently in the direction of greatest pressure."

Wheeler ('95, p. 309) states in regard to the first cleavage spindle of Myzostoma: "In Myzostoma the spindle does not conform to O. Hertwig's law, but always lies at right angles to the long axis of the often very narrow protoplasmic pillar of the egg."

Castle ('96, p. 250) states that in the division of the entoderm cells of Ciona the spindles in certain cases lie in the short axes of the cells, even when a shifting of the asters from a previous position in the long axis must have occurred to bring about this condition. Castle states that no mechanical explanation of this phenomenon offers itself, though he holds that "*other things being equal*, it is true that the spindle arises in the longest axis of the cell" (p. 231, note).

In the decapod crustacean Virbius, according to Gorham ('95), the egg is ellipsoidal in form, and the first cleavage spindle may occupy the long axis, or be more or less inclined to it, or may even be nearly at right angles to it.

The cell divisions in the germ bands of Crustacea as described by Bergh ('95), in which the spindles take the same direction for many cell generations, should be added here (see also McMurrich, '95); though the evidence from these must be weakened in the eyes of the upholders of Hertwig's law by the fact that before division the cells "wachsen nur in der Weise, das ihre Längsdurchmesser dem Querdurchmesser ziemlich gleich wird und dann tritt die Theilung ein."

The positive evidence upon the question from observations of normal cell division is thus rather scanty, though doubtless some additions might be made by a further study of the literature.

From both experimental evidence and observation of normal division the only conclusion possible is, that in some organisms the spindle *does* take a position in the greatest axis of the protoplasmic mass, apparently without regard to other factors, while in other cases the position of the spindle is determined by other factors, without regard to the form of the cell.

The result is at first thought not very satisfactory, but this is not the only organic phenomenon with regard to which such a conclusion must be drawn. A few examples will make this clear.

Stahl ('85) found that the direction of the first cleavage in the spores of Equisetum is determined by the direction of the infalling rays of light. A general statement of the effect of the direction of the light rays on cell division would take a form similar to the unsatisfactory conclusion above given for the shape of the cells.

If we leave cleavage and take up other growth phenomena, such as the direction of growth of plants and animals, such a conclusion would be reached with regard to almost every agent that ever exercises a determining power. The effect of light is to cause certain parts to grow towards it, others to grow away from it; while in other organisms the direction of growth is not affected by it at all. The same is true of gravity, of heat, and of various chemical and physical agents. (See the extended list of such cases given by Herbst, '94.) In all these cases we are dealing with *reactions to stimuli.* It is only when we attempt to make one of these agents the *only* determining factor, and expect to see it act always in the same way, as a simple mechanical cause, that our result becomes unsatisfactory.

It is evident that in this question of the relation of the form of cells to the direction of cleavage, we are dealing with a problem of a nature similar to those which I have briefly stated above. Some organisms are so constituted as to react to rays of light by growing toward them, others are not. In the same way, some cells or nuclei are so constituted as to react to the influences determining form by bringing the spindle into the longest axis of the protoplasmic mass; others are not. In each case the result is due to a reaction to stimulus, or to an action of similar nature, and not to a simple mechanical action of the agent.

In almost or quite all cases of reaction to stimuli, the result may be shown to be the accomplishment of a certain end that is of importance for the existence of the organism. The immediate explanation always takes a teleological form. It is not difficult to perceive a teleological aspect of this tendency of many cells to divide with the spindles in the longer axes. In cases where the purpose of cell division is merely to double the number of cells without alteration of form, division with the spindle in the longer axis is obviously the simplest method. A consideration of what would be the result if the opposite method prevailed shows this clearly. By continued division of a cubical cell and its products with the spindle in the shortest axis, a series of flat plates would be produced; every cleavage would bring about a greater modification in the form of the resulting cells, and cells of such form would undoubtedly be very inconvenient for the purposes of the organism. Continued division with the spindles in the long axis would result, on the other hand, in the production of cells of the same form as the parent cell. It is not remarkable, therefore, if in many cases the cells are so constructed as to respond to a change of form by a corresponding change of position of the spindle, so that the resulting cells shall be as nearly as possible of the form of the parent.

But mere increase of the *number* of cells without change of form is not the only object which can be brought about by cell division, and when other purposes are to be accomplished the cells are so constituted as to react in a different manner. Thus, I have shown that in Asplanchna divisions of cells with spindles in the short axis is the method by which is brought about the continued extension of cells in one direction, with consequent gastrulation and a later invagination of ectodermal cells. In Amphitrite, where, according to Mead, the division in the germ bands is with spindles in the short axes, this method of division is perhaps necessary to bring about the elongation of the germ bands, and the same is doubtless true in the germ bands of Crustacea. It is of course not necessary, nor is it probable, that in these cases the position of the spindle in the short axis is a reaction to the form of the cell; more probably the position of the spindle is determined without reference to this, as I have endeavored to show for the cells of Asplanchna.

The conclusion to which I have come is therefore similar to that maintained by Braem ('94), except that he seems to imply that the purpose of the cleaving cells is always the same, viz. to gain free space for the development of the products of division, whereas it appears to me that the facts indicate that the ends to be accomplished may be various, and the means by which they are brought about equally varied. This brings us to a nearer consideration of Braem's view.

(3) *Braem's theory of least resistance.* (Compare page 5.) — As just stated, so far as Braem's view is teleological, I must agree with him; but in so far as he seems to restrict his teleology to the accomplishment of a single purpose, — the attainment of the freest space for development, — it seems to me that the facts are against him. Certainly the principle of "least resistance" does not aid in understanding the cleavage of Asplanchna, where a large number of the divisions take place in what must be considered the direction of *greatest* pressure. Examination of the figures will show that, as a rule, the blastomeres in the resting stages are much flattened dorso-ventrally and extended laterally, as if subjected to great pressure; nevertheless, as shown in detail in the descriptive portion and in the discussion of Hertwig's law, when division takes place it is very frequently with the spindles in the dorso-ventral axes. The cleavage in this direction seems to have a purpose, but that purpose is not the gaining of the freest space for the development of the products of division, but the accomplishment of the process of gastrulation.

Since Braem's principle is confessedly teleological, it was probably not intended to be rigidly applicable to all cases; indeed, the author states as much. But in view of the frequent departures from the principle of least resistance, it appears necessary that the object of any given method of cleavage should be judged in each case for itself; so that Braem's contention that his principle is fitted "den Verlauf der normalen Furchung in wesentlichen Punkten zu erklären" must be considered unsuccessful. It may, by calling attention to one method in which cells react to a stimulus, "explain" the cleavage of some cells in the same sense that the growth of the stem and root of a plant may be said to be "explained" by saying that the protoplasm of one is so constituted as to react to light by growing toward it, the other, on the contrary, so as to react by growing away from it. But in other organisms the determining stimuli are of an entirely different nature, and the "explanation" must be sought anew for every organism.

I am of course fully aware that the view here put forth, that the position of the spindle must be interpreted teleologically, and in many cases as a reaction to stimulus, is not an "explanation." But I see no *a priori* ground for expecting a simple mechanical explanation for the direction of cell division, any more than we should of the direction of growth of a plant. As a matter of fact, the phenomena show that such an explanation is not at present possible for either.

(4) *Roux's theory of a compromise between the tendency immanent in the nucleus and the tendency due to the form of the protoplasmic mass.* (Compare page 6.) — As remarked above, this theory is not *definite*, in the same sense as the three foregoing, inasmuch as one of its factors — the immanent tendency of the nucleus — is of an entirely unknown character. From the foregoing description and discussion it is evident that I must agree fully with this conception. The further question comes, In how far do the phenomena in Asplanchna lead to a recognition of the second factor, — the tendency due to the form of the cells? It is evident that the form of the cell does not determine the main features of the direction of division, — the question as to whether the spindle shall be dorso-ventral or lateral in direction. But are there subordinate features in which the form of the cell does affect the position of the spindle, as held by Roux? In other words, does the spindle always lie in either the long or the short axis of the cell, and never oblique to both?

An examination of the figures will show that in the large majority of cases the latter question is to be answered affirmatively. In the earlier stages, before the great changes in the positions of cells have occurred, the dorso-ventral axis of the egg commonly coincides with either the greater or the lesser axis of the cells, so that from these cases no evidence on our question can be gained. But in later stages the crowding together of the cells results in greater or less alteration of the cell axes in relation to the axes of the egg. In Figure 68 (Plate **8**), for example, the long axis of the cell $d^{8.11}$ is not parallel with that of $d^{8.12}$; the two are wedged apart dorsally by the cell $d^{8.17}$, so that neither one points exactly to the animal pole of the egg. The two spindles are likewise at an angle with each other, and lie in the long axes of the cells, instead of exactly dorso-ventral. The same is true of the cells $c^{7.7}$ and $c^{7.11}$ in the same figure. Again, in Figure 74 (Plate **9**) the spindles of $d^{8.17}$ and $d^{8.19}$, though in general direction dorso-ventral, form an angle with each other, the one in $d^{8.17}$ being modified in position so as to lie in the longer axis of the cell, while the one in $d^{8.19}$ lies in the shorter axis of the cell. In the entoderm the same thing is strikingly true of the spindles shown in Plate **9**, Fig. 79, and Plate **10**, Fig. 83, for there the spindles form various angles with one another, all lying in the longer axes of the cells.

But these cases do not *necessarily* lead to the view that the form of the cell modifies even slightly the position of the spindle. It is possible that in each cell the axis of the spindle is determined otherwise, so that alteration of the *position* (not form) of the cell necessarily produces an alteration in the direction of the spindle. Thus in Figure 68 (Plate **8**), if the cells $d^{8.11}$ and $d^{8.12}$ are ellipsoids of fixed form in which the two ends of the spindles have predetermined positions, in case the cells are forced apart, as in this instance by $d^{8.17}$, the ends of the spindles will be forced apart to the same degree. Though we know that the cells are not ellipsoids "of fixed form," yet we also know that *the form of the cell is greatly influenced by the direction of the contained spindle.* It is possible that the cytoplasm of the cell tends to group itself symmetrically about the contained spindle, so that the direction of the spindle is the primary factor, the fact that it lies symmetrically in one of the axes of the cytoplasmic mass being a secondary result. This becomes very probable when we examine from this standpoint the change of form of the very irregular cell $d^{6.3}$, shown in Plate **5**, Fig. 37 (surface view), and Fig. 38 (section), before the formation of the spindle, and in Plate **7**, Fig. 54 (surface), and Plate **6**, Fig. 48 (section), after the formation of the spindle. In this cell, before the formation of the spindle, the shape is so irregular that it is not possible to distinguish a definite "short axis," and no plane would divide the cell into symmetrical halves. But as the spindle is formed, the cytoplasm groups itself symmetrically about it, until just before division the spindle lies in the shorter axis of the cell, and a plane including the long axis of the spindle and the centre of the egg would divide the ceil into symmetrical halves.

If this be the true explanation, then the elongation of the cells in Plate **10**, Fig. 83, in various directions, is due to the previous alteration of the predetermined spindle axes. And certainly the elongation is not greater than is naturally the result of the position of the spindle, as has been shown for other cells.

This view is strengthened by the fact that in certain cases, where apparently it is impossible for the cytoplasm to group itself symmetrically about the spindle, the latter takes a position which is oblique to the axes of the cell. Such a case is shown in the entodermic cell $d^{7.1}$ of Figure 64 (Plate **8**); the spindle lies in neither the longest nor the shortest axis of the cell, but oblique to both.

It must be said, therefore, that the cleavage of Asplanchna gives no positive evidence of any effect of the form of the cell upon the position of the spindle; on the contrary, the evidence on the whole is decidedly against it. *This, of course, cannot be generalized and applied to other organisms*, as on the other hand the observed conditions in other organisms are not capable of giving generalizations which must hold for Asplanchna. Generalizations in the field of reaction to stimuli, which includes a very large proportion of organic activities, are exceedingly unsafe and are justifiable only after exhaustive examination of the phenomena; but in these matters scarcely more than a beginning of such an examination has been made.

(5) *Heidenhain's problem of a definite angle of rotation.* (Compare page 6.) — This certainly cannot be held to have any especial significance for the cleavage of Asplanchna; it is proposed by Heidenhain as applicable to systems of tissues in the later stages of organisms. I may point out some facts which bear upon the "problem."

In the cleavage of Asplanchna, the angle which a given spindle makes with the preceding spindle may be either 0 or 90 degrees; but it is generally either one or the other, not some angle intermediate between these.

The time and method of rotation, when rotation occurs, cannot be said to be "gesetzmässig." Commonly the asters come to lie on opposite sides of the nucleus before the rotation begins, but in the cells $d^{6.1}$ (Fig. 42, Plate **5**) and $d^{6.3}$ (Fig. 37) the change of position begins at the same time with the division of the asters, so that by a separation of the asters accompanied by motions not in a straight line, the same result is attained that would otherwise be produced by a rotation *after* the asters were fully separated.

In the larger cell at the two-cell stage, the change of position of the nucleus and spindle is not due to a rotation after the two asters are formed, but to a change of position of both nucleus and aster before the aster has begun to divide.

In $d^{4.2}$ (Plate **1**, Fig. 7) the asters and nucleus at first rotate into a position which is not the final one, so that subsequently rotation in a different manner is necessary to bring the spindle into its definitive position (Plate **2**, Fig. 16).

In $d^{6.3}$ (Plate **5**, Fig. 37, Plate **6**, Fig. 46, Plate **7**, Figs. 53 and 54) the definitive position taken by the spindle is at right angles to that of the preceding spindle, so that the simplest method of formation would be the natural separation at right angles to the axis of the preceding spindle, as commonly takes place in such cases. But, owing apparently to the peculiar form of the cell (Plate **5**, Figs. 37 and 38, surface and section), the asters separate obliquely, taking up a position such that the line uniting them is parallel to the axis of the preceding spindle; and the definitive position is reached only by a later rotation through an angle of 90 degrees (Plate **7**, Figs. 53 and 54).

There is thus no regularity about the *method* by which the asters come to occupy their definitive positions at the ends of the spindles. Apparently *the early position of the asters is influenced or determined by the mechanical conditions within the cell,* whereas the later position of the spindle is largely independent of such conditions.

On the other hand, in the divisions of the ectoderm of Asplanchna, there *is* a regularity in the final angle between the axes of two successive spindles in any given "layer" of cells, the second spindle being in *all* the cells of a given layer either parallel with or else at right angles to the preceding spindle. It is thus quite possible that there may be whole systems of tissues where there is such a regularity. But the fact that the definitive position may be reached by such various means renders the phenomenon of little significance for a mechanical theory such as that presented by Heidenhain.

(6) *Sachs's view that the walls separating the cells meet one another at right angles.* — An examination of the figures, especially the sections, shows that the condition above stated is not generally complied with in the cleaving cells of Asplanchna, so that it is not necessary to enter upon a discussion of this view. Neither is the regular alternation of spindles

at right angles to one another — a theory often attributed to Sach — the rule in Asplanchna.

(7) *Rauber's theory, that the asters of the different blastomeres exercise an attraction for one another, thus influencing the direction of the spindles.* — There appears to be nothing in the cleavage of Asplanchna that would lead to such a conclusion as the above. Any attempt to explain the relative positions of asters in the different cells — in such a case, for example, as is shown in Figure 39 (Plate **5**) — by the theory of attractions and repulsions among the asters, will be found to lead to purely arbitrary assumptions as to which asters exercise attractions on others and which do not; any general statement of a positive nature will be found to be inconsistent with the facts. Moreover, the irregularities in the migrations of the asters, to which attention was especially called in the discussion of Heidenhain's "Problem of a regular angle of rotation," can with difficulty be harmonized with such a theory.

(8) *Braem's principle of equal resistance at the two ends of the spindle.* — This principle is discussed in connection with the question which immediately follows.

B. *What determines the Equality or Inequality of Cleavage Products?*

C. *What determines the Rate of Cleavage?*

Owing to the similarity of the factors supposed to determine the relative size of the cleavage products and the time of cleavage, it will be well to consider together the foregoing questions.

In regard to the first question, we have (1) the theory of Hertwig, stated on page 8, that the spindle tends to take a position in the middle of the mass of protoplasm in which it is contained, and (2) the "principle of like resistance at the two ends of the spindle," set forth by Braem, and stated on page 7. Since these two theories lead to similar results, they may be considered together.

It certainly does not aid in understanding the cleavage of Asplanchna to assume that "der Kern von vornherein das Bestreben hat, sich gleichmässig nach beiden Seiten hin auszudehnen und somit auf eine äquale Zelltheilung hinzuwirken" (Braem, '94, p. 345), nor that "der Kern stets die Mitte seiner Wirkungssphäre einzunehmen sucht" (Hertwig, '93, p. 172). No differentiation into more and less yolk bearing regions is visible. Yet the first cleavage is unequal, and the second equal in one cell and unequal in the other; the third likewise shows both methods, with a preponderance of equal divisions; and in the fourth all the divisions are again unequal. In no cleavage is there throughout an equality in the size of the two products in all the cells. The two assumptions above stated are strikingly contradicted, not only in the formation of the polar cell (Fig. 1), but also in the fifth (Fig. 35, Plate **5**) and sixth (Fig. 49, Plate **6**) cleavages of the entodermal cell ($d^{5.1}$ and $d^{6.1}$), and in the division of the entodermal cell $d^{8.2}$ (Fig. 80, Plate **10**). In these cases the spindle moves against one side of the cell, and there a small vesicle is produced, the two products of cleavage being excessively unequal. The contradiction is emphasized by the fact that in the fifth and sixth cleavages of the entodermal cell (Figs. 35, 48, and 49), although there is a concentration of yolk in one region of the cell, it bears no significant relation to the position of the spindle, and by the further remarkable fact that in the next or seventh cleavage (Figs. 64 and 65, Plate **8**), this yolk cloud passes into the *smaller* blastomere.

When one considers the method of formation of polar cell in *all* eggs, and the almost unlimited range in the comparative size of cells resulting from cleavage in a great number of organisms, the grounds for the generalization, that "der Kern stets die Mitte seiner Wirkungssphäre einzunehmen sucht," are difficult to comprehend, at least so far as they relate to the dividing nucleus. As a statement of fact for specific cases, with the word "stets" omitted, I have no fault to find with it; but as a generalization it is, so far as it relates to the dividing nucleus, meaningless. The position of the spindle within the cell must be considered to be related to the purpose of the ensuing division. It is of course probable that in many cases the primary purpose is to divide the formative protoplasm equally between the two products, and this may determine the position of the spindle in, for example, the first, second, and third cleavages of the frog's egg. But what determines the position of the spindle in the two divisions immediately preceding these, — in the formation of polar cells? It seems to have been generally overlooked, even by those who have pointed out that polar-cell formation is cell division, that the formation of polar cells must be reckoned with in any general theory of cell division.

An examination of the cleavage of many invertebrates shows that, as in Asplanchna, equal cleavage is no more the rule than unequal cleavage, even where there is no corresponding differentiation into yolk bearing and purely protoplasmic regions. The statement that the dividing nucleus tends to take a position in the middle of its sphere of action is true, if we consider the "middle of its sphere of action" to be, as it actually is, the point where it divides. But with this interpretation the statement is of course utterly without significance. The real question is, What determines the point where it divides? Why in Asplanchna does the middle of the sphere of action in the fourth and seventh cleavages of the large ventral entoderm cell lie in such a position (Fig. 16, Plate **2**, and Fig. 65, Plate **8**) as to divide the cell into parts which are only slightly unequal, while in the intervening fifth and sixth cleavages (Fig. 35, Plate **5**, and Fig. 49, Plate **6**) the middle of the sphere of action is at the periphery of the cell? Why at the first cleavage of the frog's egg is the middle of the sphere of action in the centre of the mass of formative protoplasm, whereas at the divisions immediately preceding — the formation of the polar cells — it is at the periphery of the egg?

In regard to the question what determines the comparative *rate* of cleavage the case is similar. In view of the recent discussion of these two questions — the inequality of cleavage and the rate of cleavage — in the works of Kofoid ('94, p. 196), McMurrich ('95), Lillie ('95, p. 45), zur Strassen ('95), Ziegler ('95), and others, it seems scarcely worth while to insist upon the fact that the rate of cleavage and the equality or inequality of the products are related to the future morphogenetic processes, and show in many cases no relation whatever to accumulations of yolk. Yet the so called laws, according to which these matters are determined by the distribution of yolk, are repeated in O. Hertwig's text-book on the cell (Hertwig, '93, pp. 174 and 180), and reaffirmed in the latest edition of his treatise on embryology (Hertwig, '96, pp. 67 and 84).

In Asplanchna the main facts in regard to the sequence of cleavage are as follows.

(1) The order of cleavage is, within very narrow limits, *constant*. If a number of eggs are taken showing successive stages of the division of any given cell, the series will show corresponding successive stages in the nuclear history of the other cells.

(2) There is a typical order for similar cells of different quadrants of the same egg. This order is *D*, *C*, *B*, *A*.

(3) There is a marked general tendency for larger cells to divide first. In every case where two cells of the same origin are of different size, the larger divides before the smaller.

This is a very general phenomenon, as has been repeatedly pointed out of late, even in cases where the larger cell contains the greater amount of yolk. The "law" recently formulated by Hertwig ('96, p. 67), that "die Schnelligkeit der Furchung proportional ist der Concentration des im Theilungsstück befindlichen Protoplasmas," must be considered — like the corresponding one in regard to the equality or inequality of cleavage products — as an example of the immature generalizations to which embryology has fallen heir through the accidental circumstance that the amphibian egg was for a long time the chief object for the study of cell division. It seems to be exceedingly difficult to grasp the fact, every day becoming more evident, that because a statement is true for the eggs of some of the lower vertebrates it does not follow that it must be true for the cells of all organisms.

(4) The rhythm of cleavage has an important relation to the other processes of morphogenesis. If cleavage took place coincidently in all the cells of the egg, the latter still retaining its form, there could apparently be no "rotation" of the cells upon one another, and consequently no gastrulation. The tension in all directions would be the same; none of the cells would be moulded to fit the extension of neighboring cells, and all would retain approximately the positions held at the beginning.

It would perhaps be possible to carry this into detail, and show that the *earlier* cleavage of the large ventral cell, leaving it in a resting condition, and therefore *plastic* (as indicated by a comparative study of the forms taken by resting and by dividing cells) when the other cells divide and extend, is directly favorable to gastrulation.

The question as to the factors determining the time and the equality or inequality of cleavage, it will be seen, does not at present admit of any direct simple answer. Cleavage is a part of the process of morphogenesis, and its rhythm and other features are related to the nature of the form to be produced.

D. *As to Differentiation accompanying Cleavage.*

The facts bearing upon this question to be derived from the observation of the early development of Asplanchna are few in number. The principal phenomenon to which attention must be directed is that of the segregation and migration of the cloud of granules, described on pages 25, 30, 37, and 54. As will be remembered, a concentration of granules begins in the ventral region of one of the cells at the eight-cell stage (Fig. 7) and becomes more and more marked as successive cleavages take place, till a well defined cloud of very large and distinct spherules occupies the anterior and ventral margin of the cell $d^{5.1}$ in the stages immediately succeeding the sixteen-cell condition (Fig. 32, Plate **4**, and Fig. 48, Plate **6**). Then occur the remarkable migrations shown in

Figures 49, 50, 51, and 64 (Plates **6** and **8**), until the cloud of granules is enclosed at the seventh cleavage in the smaller of the two entoderm cells (Fig. 65). This whole process shows clearly that other changes of a striking character are taking place at the same time as the division of the egg into smaller portions; evidently cleavage is not a mere separation of the egg into smaller masses, each similar to the other and to the original egg. The final destiny of this granular mass is not known, but such a peculiar and well characterized phenomenon as it exhibits cannot be considered meaningless.

The differentiation in this instance is of the kind admitted by Driesch (see page 9), in that it is cytoplasmic in nature. It is not, however, a direct consequence of the original distribution of materials within the egg; the migrations of the granules show that processes are taking place in the cytoplasm that are only indirectly connected with cell division.

We have in this case a distinctly visible differentiation accompanying cleavage. Certain other phenomena give evidence that there are likewise invisible differentiations accompanying the process.

At the division of the second "layer" of ectodermal cells in the sixth cleavage, shown in Figure 55 (Plate **7**), the two rows of cells $a^{7\cdot5}-c^{7\cdot5}$, $a^{7\cdot6}-c^{7\cdot6}$, $a^{7\cdot7}-c^{7\cdot7}$, and $a^{7\cdot8}-c^{7\cdot8}$ are produced. The cells of these two rows, as shown in Figure 61, are of the same size and the same form, having similar relations to the surrounding cells and to the axis of the embryo. Yet, as has been repeatedly stated, all the cells of one row divide meridionally and equally with spindles in the long axes, the cells of the other row equatorially and unequally with spindles in the short axes. What causes this difference?

The difference must, of course, be due either to a different stimulus from the outside, or to a different structure of the cells. The problem may be expressed clearly in this way: If one of the cells of the more dorsal row, as $a^{7\cdot8}$ (Fig. 61), could be removed and placed in the position now occupied by $a^{7\cdot7}$, in the more ventral row, would it change its method of division? That is, would it cleave equatorially and unequally, with its spindle in the short axis, like the other cells of the ventral row, instead of meridionally and equally, with its spindle in the long axis, as it actually does?

There is, of course, no way of answering this question directly. It scarcely appears probable, however, that there is such a difference in the influences affecting the two cells as to cause so fundamental a difference in the cleavage. And if there is not, the only alternative is, that there was a qualitative division, nuclear or cytoplasmic, at the preceding cleavage.

This conclusion is, of course, speculative, but the history of the cloud of granules directly proves that in Asplanchna the cleavage is accompanied by differentiation.

The recent experimental evidence, showing that in certain organisms the cleaving cells in early stages all possess the inherent capacity to produce an entire animal, has led to a rather widespread impression that cleavage has been shown to be a process of little or no significance, being merely a quantitative division of a mass into smaller masses of a similar nature. This view apparently receives confirmation from generalized statements of the results of such experiments; for example, the following from Driesch ('94, p. 69): "Es liegt also nach allem gesagten in der That kein Grund vor, in der Furchung etwas anderes als reine Zellteilung zu sehen; ja die Gleichheit der Furchungskerne ist direkt durch Versuche bewiesen." A summary of the evidence which has been adduced in regard to this matter shows that such a statement as the above conveys only a small part of the truth and must lead to error unless carefully interpreted. The evidence that cleavage is accompanied by differentiation may be summarized as follows.

(1) It is directly proved by observation that in certain cases the *nucleus* differs in structure in different blastomeres in early cleavage stages, and that *this differentiation is correlated with a different fate of the differing cells.* This Boveri has shown for Ascaris megalocephala (Boveri, '94), and Meyer ('95) for certain other nematodes.

(2) It is directly proved by observation that in certain cases the *cytoplasm* of the different cleavage cells in early stages is of a different structure, reacting differently to chemical reagents, and *this difference is correlated with a different fate of the different cells.* Thus, in the sixteen-cell stage of Nereis, "the somatoblast can always be recognized at a glance" from its different color (Wilson, '92, p. 390). A similar fact has been shown above in regard to the cytoplasmic differentiation in Asplanchna, but here I have not been able to determine the fate of the cell which receives the differentiated granules.

(3) It has been shown that in many cases the different blastomeres of early cleavage stages give rise to definite structures in the adult. This fact in itself of course admits of two interpretations, but taken in connection with the facts stated under (1) and (2) it becomes of great significance.

(4) It has been shown experimentally, that in some organisms sepa-

rated blastomeres give origin to *parts* of the embryo only. The most complete and satisfactory cases are those of ctenophores as described by Chun ('92) and confirmed by Driesch und Morgan ('95), and of the gasteropod Ilyanassa, by Crampton ('96).

It is difficult to conceive how a more complete demonstration could be possible, that cleavage is accompanied in many cases by differentiations which are not expressed by the phrase "reine Zellteilung," and that these differentiations are of the utmost significance for the future development of the organism. Any amount of evidence that in *other cases* there is no differentiation cannot in the least shake confidence in this demonstration.

2. Gastrulation.

In addition to the problems bearing directly upon cleavage, the plan of the present work included a study of some of the later morphogenetic processes, affecting *masses* of cells and leading to the differentiation of organs, in order to determine the relation of cleavage to these. Of these processes, gastrulation and the ensuing invagination of ectodermic cells to form the pharynx (Zelinka, '91) were studied. These are in reality parts of a single process, so that they may be treated of together under the title of Gastrulation.

In regard to the relation of cleavage to gastrulation, the result is evident from the account given in the descriptive portion of this paper. No separation of the two processes is possible; gastrulation is an accompaniment and a consequence of cleavage. At the passage from the four-cell stage to the eight-cell stage begins a displacement of the blastomeres; this displacement, or "rotation," continues in later cleavages in the same direction, and is still in operation at the latest stage examined, when it is no longer possible to follow the development cell by cell. As one of the phases of this displacement during cleavage, the large ventral cell of quadrant *D* gradually moves inward, followed later by a similar transference of the ventral cells of the other quadrants to the inside. The entire process has been followed step by step in the descriptive portion of the paper, so that it is not necessary to go into details here. In its general features the process is as follows. As the ectodermal cells begin to pass into the karyokinetic condition, they withdraw their more internal parts and increase in surface extent. The egg as a whole retains its form and size, so that the withdrawal of the internal parts of one cell necessitates an inward movement on the part of others; the result is a gradual inward migration of the ventral cells.

The inward movement of the large cell of quadrant *D*, rather than that of the other cells, seems due to several causes: — (1) The inequality of the cells. The large ventral cell having a much greater radius of curvature has less surface tension, and therefore may more easily change its form. (?) It thus yields to pressure, and fits itself to the changing form of the smaller cells. These are thus able to creep over it, as it were, and surround it. The greater quantity of cytoplasm in the entoderm cell as compared with the size of the spindle seems also to result in less change of form at the time of karyokinesis. The large cell, in virtue of its mere *size*, conducts itself on the whole *passively* with relation to the more active smaller cells. (2) The sequence of cleavage is possibly connected with this. At a given cleavage the large cell divides first, so that, when the karyokinetic stretching of the other cells takes place, the entodermic cell is in a resting condition, and therefore passive. (3) The direction of the spindles, which is prevailingly dorso-ventral, results in a continued dorso-ventral extension of the cells, so that invagination would naturally take place at one of the two ends. The developing egg may be likened to a fountain in which there is an upward movement within, an outflow above, at the animal pole, and a downflow about the periphery.

The enclosure of the large ventral cell of quadrant *D* is what has been considered gastrulation proper by Zelinka and Tessin, only the products of this cell being spoken of as *entoderm*. But after this enclosure is complete the process continues, unchanged in character, the ventral cells of the other quadrants following that of quadrant *D* to the inside of the embryo, as shown in Figures 76–79 (Plate **9**).

A necessary condition for all this displacement is of course the retention by the egg as a whole of its form and outline. If the blastomeres should separate and project above the general level, in the manner that is common for the cells of mollusks (see the figures of Unio by Lillie, '95) at the time of karyokinesis, no compensating inward movement of the other cells would be necessary, and apparently therefore gastrulation would not take place. The retention of the regular form appears thus to be of the highest importance for the development, and the question arises as to how this form is preserved. As previously stated, no membrane is visible; and any uniform force, such as surface tension or a centripetal attraction, would produce a spherical instead of an ellipsoidal form. The development of the egg proceeds as if it were enclosed in a rigid mould of oval or ellipsoidal form, so that the contents of the mould are rotated, while the form is retained. The retention of this shape seems to me inexplicable on any simple mechanical ground; the form at this stage apparently must be judged from the same standpoint as that of the adult, which no one would attempt to refer to a simple mechanical principle. Of course the assumption of the presence of a non-elastic non-extensible membrane of ellipsoidal form, which later becomes elastic and extensible, would explain the retention of the shape, and is open to any one who chooses to make it. But several facts speak against this view, aside from the general improbability of the existence of a membrane of such peculiar and changing qualities: — (1) The negative evidence that no such membrane can be demonstrated in preserved material. (2) In the sea-urchin and in Amphioxus, as shown by Driesch ('93) and Wilson ('93), development takes place as well when the membrane is removed as when present. This of course does not show that the same is true for Asplanchna, but it does show that the importance of the egg membrane has been overestimated for some cases. (3) In the rotifer Callidina, investigated by Zelinka ('91), the egg is of the same form as in Asplanchna, yet the cells sometimes put forth short amœboid processes, which of course would be impossible with a close membrane. (4) In another rotifer, Melicerta ringens, the egg is not a regular oval or ellipsoid of rotation, but one side is flattened while the other is curved, and this irregular form is retained during the shifting of the blastomeres, as is the case in Asplanchna (see the figures of Zelinka, '91, and of Joliet, '83). Such a form would not be preserved even by such a non-elastic membrane.

The facts given under (3) and (4) seem to me to render entirely inadmissible the explanation that the form of the egg in Asplanchna is due to the presence of a membrane, since this would leave the exactly similar phenomenon in the related forms Callidina and Melicerta without explanation.

The factors concerned in gastrulation may be summarized as follows: —

1. The form of the egg.
2. The change in the form of the cells at cleavage.
3. The direction of cleavage.
4. The inequality of the cleavage.
5. The sequence of cleavage. (?)

The process of which gastrulation is a part begins with the third cleavage, and continues through all the period in which it is possible to trace the development cell by cell, and apparently much later.

The process of gastrulation as above described for Asplanchna is similar to the method briefly set forth by Ziegler ('95, p. 402, note) for

Rhabditis nigrovenosa: "Ich stelle mir die Mechanik des Gastrulationsvorganges so vor, dass die Ektodermzellen nach ihrer Theilung sich abflachen und in Folge dessen ausbreiten; dabei schieben sie die Mesodermzellen über die Entodermzellen herüber. Es kann dies um so eher geschenen, da die Mesodermzellen zum Zweck der Theilung sich kugelig zusammengezogen und dabei an die Oberfläche des einschichtigen Epithels emporgehoben haben."

On the other hand, zur Strassen ('95 and '96), in his careful studies on the early development of another nematode, Ascaris megalocephala, came to an entirely different conception of the factors at work in the displacement and extension of the ectoderm cells. Zur Strassen holds that four cells of common origin constitute an "elementary mechanism," the two pairs of which attract each other in such a way as to bring about the movements which actually occur. The interaction is thought of as something having the nature of the "cytotropism" of Roux ('95). It is not necessary to discuss the matter further here, since there is no occasion to call in any such action in the gastrulation of Asplanchna. Doubtless the inter-attraction of cells exists in the rotifer, as elsewhere, but it seems to have no determining significance for the movements which take place.

3. General Considerations.

I shall next take up certain general considerations upon the mechanics of cleavage and development, which do not naturally fall under the discussion of any of the theories above considered, together with a general review of the results gained.

The egg of Asplanchna at the four-cell stage might be compared to the egg of an echinoderm, with the exception that one of the four blastomeres is much enlarged, and of a different form from the others. What variation in the cleavage will be induced by the differences in form?

As we have seen, the form of the cell in Asplanchna does not affect the direction of the spindle at cleavage. Indeed, the most characteristic feature of cleavage in Asplanchna is *difference in form and size of the blastomeres*, coupled with *identity in the direction of spindles*, in cells having the same general relations to the axes of the embryo.

In a closer consideration of the factors determining the position of spindles, it is evident from the phenomena described that the question is not a simple one, but must be resolved into (1) what determines the direction of separation of the asters; (2) what determines the position of the asters before the spindle is formed; and (3) what determines the movements of the asters into the definitive position occupied by the spindle.

(1) and (2). In regard to the first two questions, two general facts are worthy of notice.

First, there is a tendency, other things being equal, for the newly formed asters to separate at right angles to the axis of the preceding spindle, and in such a way that the asters are not to be distinguished as deep and superficial, but either as right and left, or dorsal and ventral. No explanation for this fact is apparent, and it is not in every case true. Thus in the two-cell stage the nucleus and aster in the large cell migrate to the right before the aster divides, and the separation of the two newly formed asters is not in a plane at right angles to the axis of the preceding spindle.

Secondly, the position of the asters before the formation of the spindle may apparently be modified by the simple mechanical conditions surrounding them. Thus, in the cell $d^{4.2}$ (Fig. 14, Plate **2**) the asters are modified in position almost immediately after they begin to separate, so that very soon we actually have in this cell the condition which may be considered least typical, — an inner and an outer aster (Fig. 7, Plate **1**). In the thin cell $d^{6.3}$ (Figs. 37 and 38, Plate **5**, and 46, Plate **6**) the form of the cell apparently operates to cause the two asters to separate in such a way that almost from the first the line joining them has the same direction as the axis of the preceding spindle. Such facts give the impression that before the formation of the spindle the position of the asters is undetermined, and indifferent for the general structure of the cell, except that the two asters always lie on opposite sides of the nucleus.

(3) As the karyokinetic changes take place, the asters migrate into definite positions, apparently by a rotation of the whole complex composed of the nucleus and its two accompanying asters. This rotation is into a definite *position*, without regard to either the form of the containing cell, or the previous position of the asters; that is, the *end* to be gained is constant, while the *means* of gaining it vary. Thus, at the divisions to form the sixteen-cell stage, the line passing through the asters and nucleus rotates in $d^{4.1}$ from a lateral to a dorso-ventral position, and into the greatest axis of its cell (Figs. 11, 15, and 16, Plate **2**). In $d^{4.2}$ it rotates from a position in which one aster is central, the other peripheral (Plate **1**, Fig. 7), likewise into a dorso-ventral position (Fig. 16). In $a^{4.1}-c^{4.1}$ and $a^{4.2}-c^{4.2}$ all the axes rotate from a position of

lateral extension to a dorso-ventral position, and thereby *from the greater into the lesser* axes of their respective cells (Figs. 17–22, Plate **3**). In $d^{6.3}$ the asters do not separate at right angles to the previous spindle, as commonly occurs, but the line joining them is parallel to the preceding spindle, i. e. lateral (Figs. 37 and 38, Plate **5**, and 46, Plate **6**); later, by a rotation into the short axis of the cell, the dorso-ventral position is attained (Plate **6**, Fig. 48, Plate **7**, Figs. 53 and 54). It is not possible to refer these and the other changes described in the general account of the development to any simple factors. We can refer the changes in position of the asters, and consequent manner of cleavage, only to the structure of the protoplasm and the (molecular?) processes occurring within it.

The fact that the spindles take definite positions with relation to the axes of the developing embryo, but without regard to the form of the cells, seems to indicate that there is some influence governing the egg as a whole, which is related to its form, and that the position of the spindles is regulated by this. The determining factors in the position of the spindles would therefore lie, not within any given cell itself, but outside of it. But there are certain facts which seem to render this very doubtful. As discussed on pages 70, 71, in later stages the cells become displaced by the changes taking place during gastrulation, and there is a corresponding change in the position of the spindles; they are no longer either parallel with or at right angles to the dorso-ventral axis of the egg. This is shown especially in Figures 68 (Plate **8**) and 83 (Plate **10**). If a changed position of the cell with regard to the axis of the embryo results in a correspondingly changed position of the cleavage spindle, it seems to follow that the position of the spindle is determined *within* the cell.

I do not, however, consider this conclusion as well established. It still seems *possible* that the spindles are all placed with reference to some influence resulting from the axial relations of the egg as a whole,— though not necessarily in all cases either in the dorso-ventral axis or at right angles to it.

Comparison of the conditions in Asplanchna with those reported by other observers for other organisms shows that there are cases in which the *form* of the cell *does* determine the position of the spindle. In the same way we know that there are cases in which the direction of the infalling rays of light determines the position of the spindle (Stahl, '85). But the result is not universal for either agent, so that we must hold that the effect in both cases is of the nature of a reaction to stimulus.

The form of the cell and the direction of pressure cannot therefore be used in explaining in any general way the direction of cleavage, as proposed by Hertwig and Braem. The method of reaction and the purpose of the reaction must be determined for each class of cases in itself.

A consideration of the process of gastrulation leads, though from the opposite direction, to conclusions of a similar nature. The form and direction of cleavage are related to the later morphogenetic processes. Gastrulation is a result of the method of cleavage, — and the method of cleavage must be looked upon as adapted to the purpose of accomplishing gastrulation.

The relation of the form of cleavage to the later morphogenetic processes is shown in a different way in such forms as Nereis (Wilson, '92) and Unio (Lillie, '95), where it has been possible to show the exact relation of later organs to individual blastomeres. Cleavage in many cases is itself a direct morphogenetic process, the exact method of which can be referred to no more simple mechanical factors than can the characteristic form of the adult.

I do not of course wish to generalize this statement; it is evidently true for many forms, but may not be true for all. The evidence upon which a contrary view is sometimes maintained for certain forms, as the echinoderms, seems however inconclusive. The formation of the micromères has been shown to be preceded by a differentiation in the cytoplasm (Morgan, '94), which would naturally lead to the conclusion that the micromere formation is a process having a definite signification for morphogenesis. But Driesch ('93) showed that the micromeres might be removed and a normal larva still produced. From this, however, it does not follow that the formation of micromeres is without definite morphogenetic significance, any more than it follows that the fundaments of limbs are of no morphogenetic significance because a normal larva results after the embryonic limbs have been removed from a young amphibian. The formation of micromeres apparently segregates a certain amount of substance which needs to be localized in a definite region. If this segregated material is removed, there is no evidence proving that similar material is not again segregated, at perhaps a later stage. As Roux insists, it is important to distinguish the normal method of development from induced development due to injury.

PART SECOND.—DISCUSSION OF MATTERS BEARING UPON THE MORPHOLOGY OF THE ROTIFERA.

Our knowledge of the development of the Rotifera is due chiefly to the work of Zelinka ('91). This author has given a full and careful description of the development of Callidina russeola Zel. from the egg to the adult form, with a briefer, but still extended, comparative account of the development of Melicerta ringens. Earlier works on the embryology of the Rotifera are due to Salensky ('72), Joliet ('83), Zacharias ('84), and Tessin ('86); but all of these works are incomplete and in many respects inaccurate, so that they have been almost completely superseded by the work of Zelinka. In discussing the development of Asplanchna I shall therefore restrict myself chiefly to a comparison with the results of Zelinka, drawing upon the accounts of other authors only where there is special occasion.

Since my work has been done primarily from the standpoint of cytomechanics, and not with regard to the morphology of the Rotifera, it has an entirely different aim from that of Zelinka. It thus results naturally that, in giving an account of the bearing of my studies on questions relating primarily to rotifer morphology, emphasis must be laid chiefly upon the points in which my results differ from those set forth in Zelinka's paper. The plan of my work required a more minute study of the cleavage than was demanded for Zelinka's purposes, and as a natural result I shall be compelled to criticise his account of the cleavage in regard to certain details. Furthermore, it will be necessary to show that Zelinka has been inconsistent in his account with regard to the place where the polar cell is formed, and hence is mistaken in his statement of the axial relations of the egg and embryo in the Rotifera. But all these are matters of detail, not affecting in any important way Zelinka's general conclusions, and I wish to say at the beginning that I fully appreciate the thoroughness and excellence of Zelinka's researches upon this difficult group, and make the criticisms and corrections contained in the following pages in no spirit of disparagement.

Asplanchna Herrickii de Guerne, the form upon which my studies have been made, is not closely related to any of the species of Rotifera whose development has been previously described. Callidina and Melicerta, investigated by Zelinka ('91), belong respectively to the groups Bdelloidea and Rhizota of Hudson and Gosse ('86). Rotifer and Philodina, studied by Zacharias ('84), belong also to the Bdelloidea. Brachionus, investigated by Salensky ('72), is one of the Loricata. Only Eosphora, upon which the work of Tessin ('86) was done, belongs, together with Asplanchna, to the swimming Illoricata. But even these two are widely separated, Eosphora possessing a foot and anus, like the majority of the Rotifera, whereas Asplanchna possesses neither.

The only work which has been done upon the early development of any species of Asplanchna is that by Leydig ('54) and Lameere ('90). The latter observed in the living egg of Asplancha Sieboldii the formation of the polar cell and the first and second cleavages, but did not carry his work further. Leydig ('54) observed the cleavage of the egg, and figured the four-cell stage in the same species, but does not give any detailed description. I know of no other work dealing with the early development of any species of Asplanchna.

I have examined the early stages of both Asplanchna Herrickii de Guerne and Asplanchna priodonta Gosse, of which the material collected in the Great Lakes contained about equal numbers. Asplanchna Herrickii was chosen for special investigation on account of the greater size of the embryos and adults. The development of Asplanchna priodonta was examined for comparison, and notes upon the embryology of this species have been given in connection with the fuller discussion of Asplanchna Herrickii.

1. Previous Knowledge of Asplanchna Herrickii.

It will be well to give here a brief review of previous references in the literature to the little known species Asplanchna Herrickii. It was first figured by Herrick ('84, Plate V.), and described in the explanation of plates as "flask-shaped Rotifer, hermaphrodite, with eggs and sperm," but no further description was given and no name was proposed. Herrick in a second paper ('85, p. 61) again mentions this form, but adds nothing to the description.

In 1888, Jules de Guerne ('88) reproduced Herrick's figure of the jaws, and on the basis of this held that the species was new, and proposed for it the name Asplanchna Herrickii.

Hudson and Gosse ('89) included Asplanchna Herrickii in their list of "doubtful species."

Daday ('92) admits Asplanchna Herrickii as a valid species.

Up to this time no observer since Herrick had reported finding this species. But in this same year, 1892, Wierzejski ('92) gave an account of its presence in Galicia, with a description, and figures of the jaws and the peculiar glandular organ which Herrick had mistaken for a testis. Again, in his Rotatoria (Wrotki) Galicyi, Wierzejski ('92^a) gives a figure of the entire animal, with special figures of the characteristic glandular organ, the trochal field, the jaws, and the excretory system, together with a brief description in the Polish language.

Asplanchna Herrickii was afterward reported by the author (Jennings, '94) as occurring in Lake St. Clair, and by Levander ('95) as occurring in the neighborhood of Helsingfors.

2. Development.

The unsegmented egg of Asplanchna Herrickii is similar in form to that of Callidina russeola, investigated by Zelinka, but slightly smaller, the maximum dimensions in Callidina being 130 μ by 90 μ, while the maximum dimensions observed in Asplanchna Herrickii were 97 μ by 83 μ.

No thick-shell "winter eggs" were ever observed by me in the specimens taken; possibly later in the fall these would have been found.

In regard to the details of the developmental process, reference must be made to Part First; the purpose here is merely to point out such observations as are of importance from the standpoint of rotifer morphology, noting especially any differences between my account and those of other writers.

A. Maturation.

As stated on page 13, the place of polar-cell formation in Asplanchna has a different relation to the axes of the egg from that ascribed to it by Zelinka in Callidina. In the ensuing discussion I shall, for convenience of comparison, use the orientation adopted by Zelinka; that is, what I have called the "macromere end" is anterior, the "micromere end" posterior. That side of the egg upon which later the blastopore is found, occupied in early stages chiefly by the quadrant *D*, is ventral, the opposite side dorsal. These terms have no constant relation to the terms of orientation employed in Part First.

As previously described and figured (Plate **1**, Figs. 1 and 2), the polar cell is formed near one of the ends of the ellipsoidal egg, and the place of formation is cut by the first and second cleavage furrows (Figs. 6 and 8). The same is true for Asplanchna priodonta.

In these two species of Asplanchna, therefore, the place of polar-cell formation is the same, with reference to the form of the egg, as that described by Lameere ('90) for Asplanchna Sieboldii, and by Zelinka ('91) for Callidina Leitgebii (p. 53) and Melicerta ringens (p. 117). In

Callidina russeola and Discopus synaptæ, according to Zelinka ('91, p. 53), the polar cell is formed almost exactly at one of the ends of the ellipsoidal egg, though a very little to one side. This difference is a point of little or no significance: an examination of Zelinka's figures (Taf. I. Figg. 1–5) shows that the polar cell in Callidina russeola occupies the same position with regard to the *axis of the first cleavage spindle* as it does in the three species of Asplanchna. Possibly the egg of Callidina russeola is forced by the shell to take such a form that the axes of the egg, as indicated by the first cleavage spindle, do not coincide with the apparent axes indicated by the shape. The place of formation of the polar cell, as might be expected, is correlated with the axis indicated by the cleavage spindle. After the first cleavage a rotation occurs in Callidina russeola, bringing the apparent axis into agreement with the real axis.

But with regard to the place of polar-cell formation in its relation to the orientation of the egg as shown by later development, a remarkable disagreement exists between the condition in Asplanchna Herrickii and Asplanchna priodonta on the one hand, and the description given by Zelinka of Callidina russeola on the other. The following is Zelinka's statement of the orientation of the egg of Callidina with relation to the place of polar-cell formation: —

"Es verdient hervorgehoben zu werden, dass von dem Augenblicke an, als das Richtungskörperchen gebildet wird, sämmtliche Richtungen im Räderthier-Eie orientirt sind. An dem Pol, in dessen Nähe das Körperchen austritt, finden wir später das Vorderende, am gegenüberliegenden das Hinterende, während die Fläche, in der es erscheint, zur Rückenfläche wird." (Zelinka, '91, p. 54.)

Accepting the later orientation of Zelinka, the above statement becomes accurate for Asplanchna Herrickii and Asplanchna priodonta if "Vorderende" and "Hinterende" are interchanged, and "Bauchfläche" is substituted for "Rückenfläche"; in other words, *the orientation of Asplanchna with reference to the polar cell is precisely the opposite of that of Callidina.* The statement for Asplanchna would read: "At the pole in the neighborhood of which the polar cell appears, we find later the posterior end, at the opposite pole the anterior end, while the surface on which it appears becomes the ventral surface." This statement, while correct if we relate the orientation of the animal simply to the *form* of the egg, as is done by Zelinka, contains one false implication. While that surface of the egg on which the polar cell is formed *does* later become the ventral surface of the animal, — the same form being retained to a late stage, — yet during the processes of development that part of the *material* of the egg immediately surrounding the region of polar-cell formation is moved to the posterior end of the egg, and, later across this and even upon the dorsal side. The same is doubtless true for the corresponding region (opposite the place of polar-cell formation, according to Zelinka) in Callidina. It marks the *animal* or *upper* pole in Asplanchna, lying at the opposite end of the egg from the blastopore during gastrulation, and is the common point of meeting for the blastomeres derived from the four quadrants of the egg. In Callidina russeola, according to Zelinka, the region where the polar cell is formed lies, not at the opposite end of the gastrula from the blastopore, but at the *dorsal margin of the blastopore,* and the cells of this region are later invaginated to form the fundament of the pharynx; the real animal pole of the egg lying at a distance from the point of polar-cell formation. The whole of Zelinka's general discussion of the early development of the rotifer egg is based upon this peculiar position of the polar cell. (See Zelinka, '91, pp. 132–135.) His general statement of the place of polar-cell formation is as follows: "Das Richtungskörperchen kommt an der dorsalen Seite des künftigen Embryo hervor, bei Melicerta dem späteren hinteren Pole näher, bei Callidina fast am späteren vorderen Pole des in beiden Fällen länglichen Eies."

The difference between our accounts is seen by comparing Figure 6 (Plate **1**) and Figure 8 (Plate **2**) with Zelinka's Figures 8, 9, and 10 (Tafel I.). In the two-cell stage in Asplanchna (Fig. 6), when the smaller cell, $\overline{AB}^2$, is turned away from the observer, who looks down upon the polar cell, the spindle in the larger cell is seen to occupy such a position that the smaller product of the division of $\overline{CD}^2$ will lie to the *right*, and in Figure 8 this condition is shown to be realized when the division has taken place, the cell C^3 lying to the right of the polar cell. In Zelinka's figures, however, the small cell II ($= C^3$), derived from the division of the larger blastomere of the two-cell stage, lies to the *left* of the polar cell, when the same orientation is adopted; i. e. with the smaller blastomere ($A = \overline{AB}^2$) of the two-cell stage away from the observer. It therefore follows that, if the position of the polar cell is dorsal in Callidina, it must be ventral in Asplanchna, *using Zelinka's orientation.* Later stages show the same contrast. Thus Figures 13 and 14 (Plate **2**), representations of the eight-cell stage of Asplanchna, show the polar cell in the position already described, (the dorsal pole of the egg being directed toward the observer,) whereas Zelinka's Figures 15, 16, and 18 of Callidina show it at the opposite pole. Figures 19, 20 (Plate **3**), 38, 41 (Plate **5**), and 59 (Plate **7**) show the polar cell at later stages in Asplanchna, and demonstrate clearly that it lies at the animal pole of the egg, opposite the blastopore.

Moreover, a careful examination of Zelinka's own work shows that the general statement above cited cannot be considered correct for all Rotifera. His general conclusions are based throughout primarily upon his more complete study of Callidina, and in his "Theoretischer Theil" he seems to have overlooked the fact that in Melicerta the place of polar-cell formation observed by himself was, not only not near the anterior end, as noted in the above general statement, *but also not upon the dorsal side.*

The egg of Melicerta is described (Zelinka, '91, p. 115) as an elongated ovoid with a sharper and a thicker or blunter end; one side is cylindrical in form, so as to appear straight in profile, while the other is swollen, presenting in profile a convex outline. Zelinka says in regard to the orientation of the egg given by Joliet: "Da ganz richtigerweise das dickere End als das Kopfende, das dünnere als das Hinterende bezeichnet wird, sowie ferner dieser Autor dessgleichen richtig die vorgebauchte Fläche als die ventrale, die cylindrische als die dorsale ansicht, so wäre die Orientirung durch diese Form des Eies eigentlich erleichtert," etc. Now, in Zelinka's figures of the maturation stages of Melicerta (Taf. V. Figg. 74–76) the polar cell is clearly shown to be formed at this *convex*, and therefore *ventral* side. Furthermore, his description of the process of maturation is as follows: "Das Keimbläschen zeigt zuerst noch seine wohlbegrenzte sphärische Gestalt (Fig. 73) und liegt etwa in der Mitte des Eies, sodann wandert es, indem es lebhaft seine Gestalt verändert, gegen den hinteren Pol, wird zu einem halbmondförmigen Fleck mit gekerbten Rändern (Fig. 74), dessen Konvexität der *Bauchfläche* zugekehrt, *welcher es sich rasch nähert.* Knapp unter der Oberfläche zerlegen die Kerben den Kern in drei eng an einander liegende ungleiche rundliche Stücke (Fig. 75), deren der Oberfläche zunächst liegendes aus dem Ei gepresst wird."[1] (pp. 116, 117.) The figures show clearly the convexity of the curved nucleus directed toward the convex ventral surface of the egg, the gradual approximation of the nucleus to that surface, and the formation there of the polar cell, as described in the above passage. In the "Erklärung der Abbildungen," these figures (73–77) are said to be "Rechte Seitenansichten," which would make the convex surface and the place of polar-cell formation *dorsal*, as required by Zelinka's general statement. But this contradicts the description just quoted, and there is other proof that the orientation of this first row of figures (73–80) of Melicerta is incorrectly given in the "Erklärung der Abbildungen." Thus, Figure 78 is said to be a "Dorsalansicht," which would bring the blastomere II ($= C^3$) upon the left side. But this blastomere is, in all other rotifers whose development is known, formed on the *right* side, and Zelinka states concerning this very figure, "Zuerst folgt der Kerntheilung die Zelltheilung in dem grossen Blastomer, die Theilungsebene steht senkrecht zur Kernspindel und schneidet ein Stück an der *rechten* Seite schief heraus (Fig. 78, II)."[1] (p. 117.) Again, Figure 79 is said to be a ventral view, whereas the same considerations as in the last case show it to be a *dorsal* view. Figure 80 is said to be a ventral view of the stage shown in Figure 78. Yet it is evidently a later stage than Figure 78; it really represents a ventral view of a stage similar to Figure 79, though the latter itself is said in the "Erklärung" to be a ventral view. In the text, Zelinka states correctly that Figure 79 is a dorsal, Figure 80 a ventral view (p. 118) of the same stage (p. 117), contrary to the statements in the "Erklärung der Abbildungen."

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[1] The Italics are mine.

In Melicerta, therefore, the polar cell is formed in the same position as in Asplanchna Herrickii and Asplanchna priodonta, and marks the animal pole of the egg.

It seems very improbable that between these three forms and Callidina there should actually be such a difference in regard to the place of polar-cell formation as is brought out by the above comparisons. Zelinka's account of Callidina is full and clear upon this point; in both his description and his figures the polar cell is traced to a late stage, when a mistake in the orientation is impossible. There seems, however, to be one opportunity for error. The polar cell in Callidina is not embedded between the blastomeres, as in Asplanchna, but lies free upon the surface of the egg. This is shown by Zelinka's figures as well as by his descriptions. On page 62 he says, "Das Richtungskörperchen hat seinen Platz, den es früher eingenommen, verlassen und liegt nun ganz auf den kleinen Zellen." The egg of Callidina is enclosed by a rigid shell or membrane, which is separated from the egg itself by a space, except at the sides. The shell retains constantly the ellipsoidal form, while the egg itself may change its form and rotate within the shell. The original place of polar-cell formation, with respect to this shell, is near one end, — the end next to which *lies later* the anterior extremity of the embryo. But immediately after the first cleavage the egg rotates within the shell through an arc of about 90 degrees, and the region of polar-cell formation is carried to the equator of the egg. The polar cell itself is shifted at the same time, and it seems possible that during this rapid rotation it may be transferred to a region of the egg different from its original position. Such shiftings of the polar cell, though to a less extent, are mentioned by Zelinka (pp. 55, 58). During the "sehr schnell verlaufendes Phänomen" of the rotation of the egg within its shell, the relatively different shifting of the polar cell might have been overlooked. This is, however, only the suggestion of a possibility, for which there is no direct evidence in Zelinka's work.

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[1] The Italics are mine.

It is to be noted that in the above discussion I have employed throughout the orientation of the egg used by Zelinka, and not that adopted in my own account of the development.

B. Cleavage.

The first cleavage in the two species of Asplanchna differs from that of Callidina russeola in being exactly transverse to the long axis of the egg. In the latter form, according to Zelinka, the first cleavage plane is oblique to the spindle, and the spindle itself is oblique to the long axis of the egg. By a change of their relative positions immediately after division, the two cells are later brought into the same position relative to each other as in Asplanchna, and even at first the cleavage plane in the two forms occupies the same position *relative to the place of polar-cell formation.* The difference thus is of little importance, except that, from a cyto-mechanical standpoint, it shows that the form of the egg does not determine the position of the first cleavage spindle. In Eosphora also (Tessin, '86) the first cleavage plane is oblique to the long axis of the egg, whereas in Melicerta ringens (Zelinka, '91) and Asplanchna Sieboldii (Lameere, '90) the first cleavage plane is transverse to the long axis, as in Asplanchna Herrickii and Asplanchna priodonta.

The second and third cleavages in the two species of Asplanchna (Plate **1**, Fig. 6, Plate **2**, Figs. 8–16) are essentially similar to the corresponding cleavages of Callidina and of other rotifers in which the development has been described. For convenience in comparing the later stages, I give here a table showing the correspondence between the cells of Asplanchna in the eight-cell stage and those of Callidina.

Asplanchna.	Callidina (Zelinka, '91).	Asplanchna.	Callidina (Zelinka, '91).
$a^{4 \cdot 1}$	a_1	$c^{4 \cdot 1}$	II_1
$a^{4 \cdot 2}$	a_2	$c^{4 \cdot 2}$	II_2
$b^{4 \cdot 1}$	b_1	$d^{4 \cdot 1}$	I
$b^{4 \cdot 2}$	b_2	$d^{4 \cdot 2}$	III

Lameere ('90) and Leydig ('54), have given figures of the four-cell stage of Asplanchna Sieboldii. Beyond this stage there are no other published figures of the cleavage of any species of Asplanchna.

In regard to the fourth cleavage (Figs. 19–30, Plates **3** and **4**), a remarkable difference is to be observed between the cleavage of Asplanchna and that of Callidina as described by Zelinka. In Asplanchna the cleavage takes place up to (and beyond) this point with the greatest regularity both as to direction of spindles and as to sequence. The first and second cleavages are meridional, the third equatorial, and the fourth again equatorial. The sequence of cleavage is in every case *D*, *C*, *B*, *A* (see nomenclature of cleavage, page 16). In Callidina, according to Zelinka, the rhythm and regularity of the process is destroyed after the third cleavage by the remarkable circumstance that the cell $d^{4.1}$ (I, Zelinka) divides twice in succession before the fourth cleavage of any of the other cells. After these two divisions of $d^{4.1}$, the six cells of the other three quadrants are said to divide in the same succession that occurs in Asplanchna, while it is not until all these cleavages are finished that the cell $d^{4.2}$ (III, Zelinka) is separated into two blastomeres. Before this division of $d^{4.2}$ takes place, the egg consists in Callidina, as in Asplanchna, of four rows of four cells each, but in Callidina the method of origin of the four cells of quadrant *D* is stated to be different from that in the other quadrants. In this quadrant the three dorsal cells (posterior, Zelinka) are said to arise by successive cleavages of the large ventral (anterior, Zelinka) cell, while in each of the other three quadrants the four cells arise by the halving of the two cells previously present.

In Melicerta, according to Zelinka, the cleavage up to this point is as in Asplanchna; the cell I ($d^{4.1}$) divides first, then III ($d^{4.2}$), then the cells of the other three quadrants. Later the cleavage of Melicerta differs from that of Asplanchna, but up to the end of the sixteen-cell stage the processes are the same in the two.

In Eosphora, as described by Tessin ('86), the cleavage is like that of Asplanchna, except in the unessential particular that his cell a'' ($= d^{4.2}$) divides before the cleavage of a ($= d^{4.1}$). The sixteen-cell stage is reached by the cleavage of the same cells as in the two species of Asplanchna and in Melicerta.

In view of the regularity of the cleavage in these four forms, one might be led to suppose that the irregularity described in Callidina by Zelinka was due to defective observation. Zelinka has noted this point with particular attention, and states that he is certain of the difference between Callidina and Eosphora, as described by Tessin. Nevertheless it is possible that the slight *time* variation in the cleavage of Eosphora may have misled Zelinka as to the point which needed especial care. In Asplanchna Herrickii and Asplanchna priodonta, in Melicerta and in Callidina, the large cell $d^{4.1}$ divides first, followed immediately (in all except Callidina, at least,) by the division of $d^{4.2}$. In Eosphora, by a slight relative delay of the cleavage in $d^{4.1}$ (*a*, Tessin), the cell $d^{4.2}$ (a'', Tessin) divides first. Zelinka states that he has observed with especial care that the first cell (IV, Zelinka) given off in this quadrant takes origin from $d^{4.1}$ (I, Zelinka). This is doubtless true; the important point, however, is the origin of the *next* cell formed. Though this also is stated to arise from the ventral cell of the series (I, Zelinka), it seems possible that Zelinka was thrown off his guard by the supposed greater care necessary for determining the exact method of the preceding cleavage, and that the statement with regard to this one is really a mistake. The cell IV in Figure 23 (Taf. II.) of Zelinka's work might be the same cell as V in his Figure 24, while the cells called III and IV in Figure 24 might have arisen by the division of the previously existing cell III ($= d^{4.2}$). This would bring the conditions in Callidina into agreement with those in Eosphora, Melicerta, and the two species of Asplanchna. This is, of course, a mere suggestion, which indeed is rendered rather improbable by the nuclear conditions in the cells under discussion shown in Zelinka's Figure 24. There can, of course, be no question about the manner of division in Asplanchna. Figure 16 (Plate **2**) shows the spindles in $d^{4.1}$ and $d^{4.2}$, and the accomplished division of $d^{4.1}$ into $d^{5.1}$ and $d^{5.2}$ is shown in Figure 19 (Plate **3**), while $d^{4.2}$ still contains a spindle. I have observed similar conditions in many other specimens.

In view of the essential similarity of the process in Eosphora, as described by Tessin, to that in Melicerta, as described by Zelinka, and in the two species of Asplanchna, as observed by me, and in view of the fact that the cleavage of the quadrant in question (*D*) in these four forms may be said to agree completely with the general plan of cleavage as exhibited in the other three quadrants, — while in Callidina the conditions in this quadrant are anomalous, — the following remark of Zelinka ('91, p. 61) seems hardly justifiable: "Da, wie später gezeigt wird, auch Melicerta in der Entwicklung unserer vorliegenden Form folgt, so muss der Vorgang bei Eosphora als eine bemerkenswerthe Verschiedenheit aufgefasst werden." As above shown, the difference between Eosphora and the other forms consists merely in a slight variation as to the relative time of cleavage of two blastomeres ($d^{4.1}$ and $d^{4.2}$), — a phenomenon which is exceedingly common both in different individuals of the same species and in closely related species, and to which little or no significance can be attached. It is Callidina which shows a "bemerkenswerthe Verschiedenheit," since here the rhythm and regularity of the cleavage are completely destroyed, if the division is correctly described by Zelinka.[1]

Beyond the fourth cleavage it becomes very difficult to compare the processes in Asplanchna with those described by other observers for other rotifers. As above described, even in the fourth cleavage one of the cells of the D quadrant ($d^{5.3}$) was formed in a different manner in Callidina, according to Zelinka, from the method in Asplanchna. This in itself makes an exact comparison of the fifth cleavage in the two species impossible. But, considering for convenience the cells corresponding in position at the sixteen-cell stage as equivalent in the two forms, we find the following to be the process in Callidina as described by Zelinka.

The first blastomere of the sixteen-cell stage to divide in Callidina is said to be the dorsal cell of the D quadrant, $d^{5.4}$ (III, Zelinka), whereas in Asplanchna the very unequal division of the ventral cell $d^{5.1}$ takes place first (Fig. 33, Plate **4**, and Figs. 35 and 38, Plate **5**). The cleavage of $d^{5.4}$ is followed in Callidina by the division of $d^{5.3}$ and $d^{5.2}$ (IV and V., Zelinka). The division is meridional, as in Asplanchna (Fig. 37), but the products are equal, whereas in Asplanchna they are unequal.

Now, according to Zelinka, the products (at the fifth cleavage) of the division of $d^{5.4}$ ($d^{6.7}$ and $d^{6.8}$, Zelinka's III_1 and III_2) are themselves divided by meridional furrows. Thus the sixth cleavage takes place in these cells before the fifth has been accomplished in any of the other quadrants.

Following this, the large ventral cell of the D quadrant, $d^{5.1}$ (I, Zelinka), divides equatorially, giving off on its dorsal side a small cell, VI, which lies between the products of the division of $d^{5.2}$.

Thus the cleavage of the quadrant D is much less regular than in Asplanchna, where the ventral cells all cleave meridionally and unequally, the dorsal cell equatorially and unequally, the direction of cleavage being the same as in the other three quadrants (see Figs. 33 and 37). In Asplanchna, moreover, the fifth cleavage in the other quadrants is well advanced before any of the divisions for the sixth cleavage in quadrant *D* have taken place.

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[1] Zelinka's statement, quoted above, that Melicerta follows the same method of division as Callidina, depends merely upon his interpretation of a real variation; the actual divisions to form the sixteen-cell stage are the same in Melicerta as in Asplanchna and Eosphora, and different from those of Callidina, as may be seen by consulting Zelinka's ('91, p. 121) description.

Zelinka does not follow the cleavage in the other three quadrants cell by cell. He states that the dorsal cells of these quadrants (all?) are divided by planes parallel to the long axis of the egg, as is the case for all but the fourth or most dorsal layer in Asplanchna, and that the ventral cells $a^{5.1}$, $b^{5.1}$, and $c^{5.1}$ (a_1, b_1, and II, Zelinka) are the last to divide. In Asplanchna, as shown in Figures 39–44 (Plates **5** and **6**), all the cells of these quadrants divide meridionally except those of the dorsal layer, which divide equatorially.

It is obviously impossible to compare in detail the cleavage in the two forms at this time, or to reduce the condition described for Callidina to the regular scheme of cleavage exhibited in Asplanchna. Certain facts are perhaps worthy of notice, as showing the possibility that the cleavage in Callidina is not so different from that of Asplanchna as would be inferred from what is indicated above. The relation of the cells in quadrant *D* are somewhat similar in Figures 30 and 34 of Zelinka's work to a later condition in Asplanchna, — a condition reached, however, in a very different way, and shown in Figures 58 (Plate **7**) and 66 (Plate **8**). Further, the unequal cleavages of this quadrant are very confusing, and easily overlooked. Zelinka's work was apparently done almost entirely on living material, which does not lend itself as well as does preserved material to precise orientation of the object, and to its rotation in such a way as to permit views from all directions. It was only by bringing together a complete series, in which the karyokinetic process in every cell was represented in various stages by several specimens, that I was able to determine absolutely the course of events here. The remarkable unequal division of the cell $d^{5.1}$ is especially liable to be overlooked; I did not observe it till the break in the rhythm of cleavage at this point set me at work upon a minute study of a series of eggs separated in cleavage conditions by very short intervals only. It is worth noting that in Callidina, shortly after the time for this cleavage to occur, Zelinka figures (Taf. II. Fig. 31) a small vesicle lying almost exactly in the place occupied by the minute vesicle given off at this cleavage in Asplanchna, viz. between the ventral cells of quadrants *A* and *B* (a_1 and b_1, Zelinka). Zelinka considers this to be the polar cell, although at a previous stage he had observed that the polar cell had become displaced and now lay farther dorsad, on the outer surface of the smaller cells of the egg. The condition shown in his Figure 31 he ('91, p. 62) considers to be an exception. Later, he states that the polar cell becomes surrounded by small spherules, indicating that it is degenerating and falling to pieces. As shown in my Figures 51 and 52 (Plate **6**), the vesicle $d^{6.2}$ produced by the division of $d^{5.1}$ in Asplanchna also becomes surrounded by large granules or spherules; but these are not of the nature assumed by Zelinka; they are the result of a concentration of granules in the ventral cell $d^{6.1}$, traceable from the eight-cell stage onward. In view of these facts, it seems possible that a similar division actually takes place in Callidina, and that the small cell lying between a_1 and b_1 in Zelinka's Figure 31 is the small product of this cleavage, — the equivalent of $d^{6.2}$ in Asplanchna.

Tessin, in his study of Eosphora, also failed to follow the cleavage in detail to the 32-cell stage. He ('86, p. 282) speaks of "fortgesetzte Aequatorialtheilungen" of the cells in the three smaller quadrants; his figures show the three quadrants composed each of a single row of six cells (Figs. 22 and 23). This corresponds to the condition in Asplanchna at a time when the dorsal cells ($a^{5.4}-c^{5.4}$) have divided equatorially, but when the remainder of these three quadrants are as yet undivided. Next, all the cells, except the large ventral cell $d^{5.1}$, are said to divide meridionally. It is probable, therefore, that the formation of the minute cell by the division of $d^{5.1}$ was overlooked, and that the cleavage is essentially as in Asplanchna. The cells of quadrant D are said to divide unequally at this cleavage, as is also the case in Asplanchna.

The sixth and later cleavages of the ectoderm have not been studied in detail by other observers, so that a comparison of my results with observations on other forms is impossible. Diagrams of the sixth, seventh, and eighth cleavages for Asplanchna are given on pages 41, 46, 48, and 53, that for the eighth cleavage being incomplete.

The divisions of the entoderm cells have been followed somewhat further by Tessin and Zelinka, so that for these a comparison may be made.

Nothing comparable to the unequal fifth and sixth cleavages of the entoderm cell (forming the small vesicles $d^{6.2}$ and $d^{7.2}$), shown in Figures 38 (Plate **5**) and 49 (Plate **6**), have been reported by other observers.

Later than these the cleavage of the entoderm in Eosphora (Tessin, '86) takes place as in Asplanchna (Figs. 64, 65, and 76–83, Plates **8–10**) up to a stage comparable with that shown in Figures 77 and 78 (Plate **9**), except that no cleavage of the smaller dorsal cell $d^{8.2}$ corresponding to the unequal division which I have shown in Figure 80 (Plate **10**) was observed by Tessin. He did not follow the divisions of the entoderm further.

In Callidina a division takes place in the same manner as the seventh in Asplanchna (Figs. 64 and 65, Plate **8**), separating $d^{8.1}$ and $d^{8.2}$. The cleavage of $d^{8.1}$ into $d^{9.1}$ and $d^{9.2}$ also follows, as described above for Asplanchna.

An unequal cleavage of $d^{8.2}$, as shown in Fig. 80 (Plate **10**), was not observed in Callidina. The cleavages which next ensue are described by Zelinka as variable. The two cells corresponding to my $d^{9.1}$ and $d^{9.2}$ divide in the same direction as the corresponding cleavages of Asplanchna (Fig. 76, Plate **9**, and Fig. 81, Plate **10**), but the dorsal cells $d^{10.2}$ and $d^{10.4}$ are smaller than the others. The cell $d^{9.4}$ (*e*, Zelinka) divides by two successive divisions, at right angles to each other, into four cells; one of these divisions corresponds to that indicated for this cell in Fig. 83 (Plate **10**), while the other is at right angles to this. The order in which these cleavages occur in Callidina is, however, variable.

According to Zelinka, each of the four cells corresponding to my $d^{9.1}$, $d^{9.2}$, $d^{9.3}$, and $d^{9.4}$ now divides into three parts, but the details of these cleavages are not given.

In Melicerta the cleavage of the entoderm is traced by Zelinka to a four-cell condition, but the process is entirely different from that in Asplanchna, Eosphora, and Callidina, so that it would not be of interest to review the facts here.

The process of gastrulation takes place in Callidina and Eosphora, and probably in all other Rotifera, in a manner essentially similar to that in Asplanchna; the large ventral cell of the left posterior quadrant is enveloped by the other cells during the process of cleavage, and becomes the entoderm.

C. Summary on Maturation and Cleavage in the Rotifera.

In general, the following facts are shown for the early development of *Asplanchna*, as compared with previous accounts of the development of Rotifera.

1. The polar cell is formed at the animal pole of the egg, at a point opposite that where the blastopore is later found, and not at the dorsal or anterior margin of the blastoporic region, as stated by Zelinka for Callidina and Melicerta.

2. A much greater regularity, and in a certain sense symmetry, are shown in the direction and rate of cleavage than has been shown for

other Rotifera. Cell lineage is traced to a much later stage than has been done for other rotifers.

3. In other respects the development of Asplanchna, so far as observed, agrees in general with that of Callidina as described by Zelinka ('91). The development of organs was not traced in Asplanchna, the purpose of the work lying chiefly in the domain of cyto-mechanics.

PART THIRD.—MATERIAL AND METHODS.

The material for the studies here presented was collected by means of towings from Lake Michigan and certain small lakes connected with it, in August and September of 1894. Such towings were killed and preserved by a variety of methods. For killing, the following reagents were tried: (1) Flemming's stronger chrom-osmo-acetic mixture; (2) Kleinenberg's picro-sulphuric mixture, weaker solution; (3) Henneguy's fluid, consisting of Kleinenberg's weaker fluid plus 10% glacial acetic acid; (4) picro-nitric acid; (5) alcoholic corrosive sublimate; and (6) a mixture of corrosive sublimate and formalin. The best results were gained by the use of Flemming's mixture. The eggs were considerably darkened, but this defect was easily corrected by bleaching with chlorine generated from chlorate of potash and HCl. Henneguy's fluid and picro-nitric acid also gave good results. By alcoholic corrosive sublimate the eggs were commonly shrunk, and with Kleinenberg's fluid the shrinking was excessive. The towings after killing were preserved partly in 80% alcohol, and partly in a mixture of equal parts of glycerine, alcohol, and water. Both these preservatives gave satisfactory results.

As is well known, the development of the embryo takes place in Asplanchna within the body of the adult. The developing egg lies in the posterior part of the body of the mother, enclosed in the greatly distended oviduct or uterus, and with the ovary of the adult closely applied to it. It was necessary to pick out the Asplanchnas one by one from the quantities of Crustacea and other plankton with which they were mingled. This was done by using capillary tubes. It was necessary, moreover, to assort them with respect to the state of development of the contained embryo, if an embryo were present. This is a process involving great labor, as, in order to determine even approximately the stage of development of the embryo, it is necessary to examine the animal with the compound microscope. The majority of the specimens contain an embryo; not rarely two are present, in different stages of development, and in a single case I observed three.

In order to study the eggs, it is of course necessary to dissect them from the mother. This, again, is a tedious and delicate process, and it is rarely possible to free the egg entirely from the closely applied oviduct and ovary. This fact causes excessive trouble later, since the fragments of oviduct and ovary attached to the egg prevent one's placing it in any desired position or rolling it about at will, under a cover-glass.

For surface study of the early stages the eggs were then mounted in glycerine under a cover-glass supported by bits of capillary tubing thick enough to allow free motion to be given to the object. It was found impossible to use to advantage any stain for this study, because all the stains tried colored the cytoplasm more than the nucleus, and made the egg so opaque that cell boundaries and nuclei could not be distinguished. For the stages from one to about sixteen cells, eggs fixed in Flemming's solution are the best, as the slight darkening produced by this reagent is of advantage in stages where the egg is cleft into but few cells. For later stages this darkening is a disadvantage; eggs killed by other methods, or bleached after fixing with Flemming's fluid, must be used.

The eggs were moved about by rolling the cover-glass on its rollers, and drawings were made of different views thus obtained. It is here that the ovary and bits of oviduct attached to the egg cause infinite delay and vexation, in preventing the eggs from rolling easily or resting in any except certain positions. The time required for the work is certainly doubled, perhaps more than doubled, by this.

With early stages, camera drawings can be made at once from the egg after a favorable position is gained; but after the egg has reached a stage of about thirty cells, it is necessary first to roll the egg and make many tentative free-hand drawings of the different surfaces, until together they show the whole surface of the egg and the relation of every cell to all surrounding cells. The egg is then oriented and a camera figure made which shows the exact form of the cells in the middle region of the upper surface, and the position of *all the nuclei* of that surface. The cell boundaries about the periphery corresponding to these nuclei are then supplied from the free-hand sketches. This method, while not giving *mechanical* accuracy for the form of the cells about the periphery of a late stage of cleavage, does permit of complete accuracy so far as the relations of cells to one another are concerned; any other method with eggs in which the cell boundaries are so faintly marked on the surface is impracticable.

Sections were made of numbers of eggs, but optical sections are much more instructive, permitting exact orientation and revealing the structure fully as well as actual sections, so that most of the figures in which sections are represented were made from optical sections.

In the descriptive portion of this paper, details have been given of the movements of asters, nuclei, and other cell contents, as well as of the cells as units. As the entire account was gained from a study of preserved material, the question is a justifiable one, — Is there sufficient evidence that the movements actually occur as above described, or are the stages figured and described merely chosen at will from a mass of material and arranged arbitrarily in series?

The number of eggs used in determining the course of events in a given cleavage has been stated in several cases in the text. Thus, 31 eggs were studied containing more than one and less than five cells; 42 containing more than seven and less than sixteen, etc. In all, more than 250 eggs from Asplanchna Herrickii and 50 from Asplanchna priodonta, between the single cell stage (Fig. 1) and the stage containing five entoderm cells (Fig. 83), were mounted in glycerine and studied. Each egg, of course, came necessarily from a different individual, — since, where two embryos were present in the same adult, one at least had passed to a stage in the formation of organs. Of many of these eggs examinations were made which may be called exhaustive; i. e. every cell with its nuclear conditions was carefully *figured*. Thus, from the egg of which Figure 68 (Plate **8**) gives one view, at least twenty drawings were made, though but one is shown in the plates. The figures given, therefore, represent by no means even a considerable part of the evidence upon which the description is based. After determination of the exact order of events, drawings of typical cases were selected for illustrating the paper.

The determination of the sequence of the stages observed is greatly lightened by the almost entire constancy in the relative order of events in the different cells. Very slight variations occur in regard to certain processes, as in the case of the migration of the cloud of granules, as mentioned in the Explanation of Plates, under Figure 51. But, in general, a number of eggs representing a series of events in a given cell show corresponding series of events in the other cells. It is not necessary, therefore, to rely upon the conditions within the cell under examination for determination of the sequence of stages in this cell. Even this would probably be possible, however, from the fact that the nucleus in any cell increases in size steadily from the time the cell is formed to the beginning of the transformation of the nucleus and asters into the spindle figure — so that the relative size of the nucleus in the same cell from different eggs gives a measure of its relative age.

An illustration will make clear the method used. Perhaps the most difficult problem was presented by the movements of the asters and nuclei in the two large ventral cells of the quadrant *D*, at the fifth and sixth cleavages. These cells are $d^{5.1}$ and $d^{5.2}$ before the fifth cleavage; $d^{6.1}$ and $d^{6.3}$ *after* the fifth cleavage. Figure 31 (Plate **4**) shows the position of the asters in all the cells of this quadrant in the resting sixteen-cell stage. Figure 32 shows the nuclei in quadrant *B* in the same egg, as seen in a longitudinal section. In the egg shown in Figure 33 the spindles are already completed in quadrant *D*, indicating that this egg is older than that shown in Figures 31 and 32. Figure 35 (Plate **5**), a ventral view of this stage, shows that the nuclei in $a^{5.1}$ and $b^{5.1}$ are much larger than the nuclei in the corresponding cells of Figures 30 and 31, — which likewise indicates that this is an older stage than is represented in the latter figures. Figure 35 shows the exact antero-posterior position of the spindle in $d^{5.1}$, while in the other quadrants the nuclei are shown to be still in a resting condition.

Figures 37 and 38 together show all the cells of this quadrant during or just after division, the four dorsal cells being still connected by interzonal filaments. It is therefore a stage *later* than that shown in Figures 33 and 35. This is in agreement with the larger size of the nuclei in quadrant *A*, Figure 37, as compared with those of quadrant *A* in Figure 33, and also with the presence of a spindle in $a^{5.4}$. In this egg the nucleus in $d^{6.1}$ (Fig. 38) has resumed its nearly spherical form, and at the side of the cell where the anterior end of the spindle was located (Fig. 35) is a small vesicle, $d^{6.2}$ (Fig. 38). This represents one product of the division.

In $d^{6.3}$ at this stage (Figs. 37 and 38). the single aster is slightly extended in a direction which is oblique to both the longer and shorter axes of the cell.

The spindles in the cells of quadrants *A*, *B*, and *C* in Figures 39–42 (all from the same egg) prove that this is a later stage than that last considered. In this egg the line joining the two asters in $d^{6.1}$ (Fig. 42) is oblique to the antero-posterior plane of the embryo, and nearly dorso-ventral.

In the egg shown in Figures 43–46, division is completed in some of the cells of quadrants *A*, *B*, and *C*, proving this to be a later stage than those shown in Figures 37–42. In this egg the two asters in $d^{6.3}$ (Fig.

46) are at opposite sides of the nucleus, the line joining them being parallel to the lateral axis of the embryo.

In the egg seen in Figure 53 (Plate **7**), the fifth division is *finished* in all the cells of the egg, (as shown by the study of the other quadrants, which are not figured,) so that this is a later stage than that shown in Figures 43–46. The asters in $d^{6.3}$ have taken an oblique position.

In the egg of which Figures 48 (Plate **6**) and 54 (Plate **7**) are representations, the nuclei in the recently formed cells of quadrants A, B, and C have enlarged, and the spindle is completely formed in $d^{6.3}$ (being dorso-ventral in position). Both of these facts show that the egg is older than the one shown in Figure 53. In this egg (Fig. 48) we find that a spindle is present in the entoderm cell $d^{6.1}$, occupying nearly the position foreshadowed by the position of the asters in Figure 42, and almost exactly the same position as the spindle at the foregoing division (Fig. 35).

The egg seen in Figure 49 is still older, as shown by the presence of spindles in $d^{6.5}$ and $d^{6.7}$ (seen endwise), and the advanced condition of cleavage in $d^{6.3}$. Here $d^{6.1}$ is just dividing, forming $d^{7.1}$ and the second small cell, $d^{7.2}$.

Figure 50 is older than Figure 49, since $d^{6.5}$, $d^{6.7}$, and $d^{6.8}$ have divided. In this egg we find that $d^{6.3}$ has been separated into two cells, $d^{7.5}$ and $d^{7.6}$, and there is a second small vesicle, $d^{7.2}$, in the position where it was seen in the process of formation in Figure 49.

The above is sufficient to illustrate the method of work; the rest of the account might be analyzed in the same way. It is important to remember, however, that the description is not based merely upon the cases figured. Thus, for the processes just analyzed, more than thirty eggs, showing various phases of the changes occurring, were studied, while only eleven different eggs are represented in the figures of these stages.

The foregoing work was done in the winters of 1894–95 and 1895–96, in the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard University. It gives me pleasure to acknowledge my great indebtedness to the Director of the Laboratory, Professor E. L. Mark, for advice and assistance which have been of the greatest value to me throughout my work.

GENERAL SUMMARY.

A. Observations.

1. Many divisions take place during the cleavage of Asplanchna in which the spindle lies in the *shortest axis* of the cell, in the direction of *greatest pressure*, and the ensuing division results in the production of contact surfaces of *greatest area.*

2. In the cleavage of the ectoderm of Asplanchna any cell of any one quadrant cleaves in the same direction as the corresponding cell of the other quadrants, though the forms of the corresponding cells may vary excessively. Conversely, cells of the same form and with similar relations to surrounding cells, but belonging to different layers or series, may divide with spindles in exactly opposite directions.

3. The entodermal cell follows the same rhythm and direction of cleavage as the other cells, so long as it remains on the exterior and thus corresponds in position with other cells of the egg. When it becomes enveloped by the other cells, so as to come into different relations with the axis of the embryo, its plan of cleavage changes, showing no definite relation to that of the ectoderm.

4. All the cleavages in the ectoderm are to a late period either equatorial or meridional, so that the position of any given spindle is either parallel or perpendicular to that of the preceding spindle.

5. There is no regular alternation in the direction of spindles. Equatorial cleavages may follow successively for three or more generations, and the same is true of meridional cleavages.

6. The position occupied by the two asters after they have passed to opposite sides of the nucleus does not indicate the direction of the ensuing spindle. This may occupy the position indicated by the asters, or the definitive position may be gained by a rotation of the asters and nucleus at the passage into the karyokinetic condition.

7. There is no "regular angle of rotation" (Heidenhain) in a mechanical sense, since (a) in cells of different layers, in one case the angle may be zero, in the other case 90 degrees; and (b) even in cells where the direction of the previous spindle and the direction of the following spindle are the same, the asters may move in an entirely different manner. In one cell the rotation may be directly through an angle of 90 degrees, and in a single plane, while in another there may be complex movements and rotation successively in different planes.

8. The position and movements of the asters in the resting stage seem partly determined by the form of the cell.

9. The rotation of the nucleus and asters into the definitive position at the time of karyokinesis often takes place *from the longer into the shorter axis of the cell,* and apparently from the direction of least pressure into the direction of greatest pressure.

10. The form of the cells in many cases does not conform to the law of minimal surfaces, being (a) changeable, and (b) even in the resting stage widely at variance with the conditions required by the law.

11. Many of the cleavages are unequal, sometimes extremely so, but the inequality shows no significant relation to accumulations of yolk material. (See 16.)

12. The sequence of cleavage is (within very narrow limits of variation) constant, and shows no relation to accumulations of yolk. There is a general tendency for larger cells to divide faster, but not all the facts regarding the succession of cleavages show relation to the comparative size of the cells.

13. In the resting stage the cells seem to be passive, taking whatever form is impressed upon them by the surrounding cells. As the cell passes into the karyokinetic condition it becomes more rounded, the cytoplasm tends to group itself symmetrically about the spindle, and the cell elongates in the direction of the spindle.

14. The spindle generally (not always) lies in either the longest or the shortest axis of the cell, as maintained by Roux. But apparently this is due in Asplanchna to the fact that the cytoplasm tends to group itself symmetrically about the spindle.

15. A change of the relation of a cell to the axes of the egg, as by a displacement due to the other cells, results in a change of the position of the spindle with reference to the axes of the egg.

16. During cleavage a cloud of granules is segregated in a portion of the cell which is to form the entoderm; this mass passes from the anterior and ventral side of the entoderm cell to its posterior and dorsal side, and is there separated off at the seventh cleavage into the *smaller* entodermal cell.

17. The egg retains its ellipsoidal form throughout all the processes of development, up to a late stage, though as cleavage progresses the blastomeres shift extensively their positions with relation to this form. This retention of the ellipsoidal form by the egg cannot be referred to any simple mechanical factor. (See pages 81, 82.)

18. Gastrulation accompanies cleavage, and advances step by step

with the withdrawal of the deep parts of the peripheral cells and their dorso-ventral extension, consequent upon frequent equatorial divisions.

19. As to facts bearing upon the special morphology of the Rotifera, —

(a) The polar cell is formed at the animal pole of the egg, at the point opposite that where the blastopore is later found, and not at the dorsal (or anterior) margin of the future blastoporic region, as stated by Zelinka ('91) for Callidina.

(b) The cleavage of Asplanchna was traced to a later stage than has been done for other rotifers. A much greater regularity, and in a certain sense symmetry, are shown in the direction and rate of cleavage than has been shown for other species.

B. Conclusions.

20. It results from 1, 2, 3, 5, 7, and 9 that the direction of cleavage is not determined by any simple mechanical factors or relations of form. Specifically, the course of cleavage in Asplanchna is inconsistent with any general validity of (1) Hertwig's law of the spindles in the longest axis of the protoplasmic mass, (2) Berthold's law of least areas, and (3) Braem's and Pflüger's principle of least resistance.

21. It results from 11 that no simple factor can account for the equality or inequality of the cleavage. Specifically, the conditions in Asplanchna are inconsistent (a) with Hertwig's view that the dividing nucleus takes a position "in the middle of its sphere of action," so far as that expression has any definite significance, and (b) with Braem's principle of "like resistance" at the two ends of the spindle.

22. It results fron 12, as well as from a comparison with the cleavage of many other invertebrates, that no simple factor, such as greater or less quantity of yolk, will account for the sequence of cleavage.

23. It is a natural conclusion from 15 and the latter part of 14, that the direction of the spindle is not due to an influence in the egg as a whole, connected with its axial relations, but is determined within each cell itself. However, I do not consider this conclusion at all well established.

24. It results from 5, 6, 7, 8, and 9 that the problem as to what determines the position of the spindle is resolvable into several: (a) What determines the direction of separation of the newly formed asters? (b) What determines the position of the asters during the resting stage

of the cytoplasm? (c) What determines the rotation of the asters and nucleus as the cell passes into the karyokinetic condition?

25. It may be concluded from 20, 21, 22, and 24 that the final position of the spindle and manner of cleavage are causally determined by processes — of an unknown character — taking place within the protoplasm.

26. The definite relation of the position of the spindle to external conditions observed in some cases — such as to the form of the cell, the direction of pressure (?), and the direction of the incoming rays of light — is to be interpreted as a reaction to stimulus, dependent in every case upon the specific structure of the protoplasm, and variable with that structure.

27. The manner of division is related to the purpose to be attained by the given division, and to the general morphogenetic changes in the organism. In Asplanchna the method of cleavage is adapted to bringing about gastrulation.

28. It follows from 16 that cleavage is not merely a quantitative division into similar units; it is accompanied by other developmental processes, some of which are distinctly traceable.

29. Gastrulation in Asplanchna is not a process distinct from cleavage, but is an accompaniment and a result of cleavage. The process of which it forms a part begins at the third cleavage and is not finished until much later than what is commonly spoken of as gastrulation proper.[1]

30. Gastrulation in Asplanchna may be analyzed into several factors.[1]

(a) The form of the egg, or the influences determining it.
(b) The direction of cleavage.
(c) The inequality of cleavage.
(d) The sequence of cleavage (?).
(e) The changes in form taking place as the cells divide.

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[1] It may be well to state expressly that I do not consider the above as in any sense a general explanation of the process of gastrulation. My aim has been to give as nearly as possible a correct account, from the standpoint of developmental mechanics alone, of the facts in regard to the early development of a single form. The origin of the process of gastrulation in phylogeny is not touched by this account. It is a common phenomenon in the organic world, that the same end is accomplished by different means in different cases; doubtless in many forms gastrulation is brought about in a way that bears no resemblance to the process in Asplanchna. In general, the whole question of the origin of processes to which an end or purpose can be assigned lies entirely without the field of the present paper.

All of these must, according to 17, 25, and 26, be considered as determined by the unknown (molecular?) structure and activities of the protoplasm.

31. It follows from 30 that the early development of Asplanchna, to a stage somewhat beyond gastrulation, may be analyzed into two factors: (1) the influences determining and preserving the form of the egg as a whole, and (2) processes occurring in consequence of the specific (molecular?) structure and activities of the protoplasm.

Both of these factors, which perhaps should be considered as different manifestations of one, are from a causal-mechanical standpoint, entirely unknown. "Damit werden die causalen Bedingungen der Entwicklung vorzugsweise in das Moleculargeschehen verlegt und entziehen sich vorderhand grossentheils unserer weiteren Erforschung." (Roux, '85^{a}, p. 427.)

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EXPLANATION OF PLATES.

All the figures represent preparations of the eggs of Asplanchna Herrickii de Guerne, except Figure 29, Plate **4**, which represents the egg of Asplanchna priodonta Gosse. All were drawn, with the aid of the Abbe camera lucida, to a magnification of 525 diameters.

The four blastomeres of the four-cell stage are distinguished by different colors, and the same color is retained throughout for all the cells (constituting a "quadrant") derived from each of the four blastomeres thus distinguished. The quadrant *A* is blue; *B*, orange; *C*, yellow; and *D*, red.

The prominent granulations in the ventral portion of quadrant *D* are figured; but all other granulations are omitted, except in the case of Figure 7, where the general granulation is also represented, though somewhat diagrammatically.

For an explanation of the system of nomenclature used in lettering the cells see page 16. In some cases for want of room the letters have been omitted, the exponents only being expressed. In such cases the color indicates to which quadrant the cell belongs.

In all the figures where it is possible, the animal pole of the egg is above, the ventral pole below. In views of the dorsal or ventral poles of the egg, the anterior end is above. Unless otherwise stated, figures represent surface views of more or less transparent eggs; these are shaded, whereas sections — optical or actual — are not shaded.

ABBREVIATIONS.

bl'po.	Blastopore.	*cl. pol.*	Polar cell.	*pol. anm.*	Animal pole.

PLATE 1.

Fig. 1. Egg showing the maturation spindle.

Fig. 2. Egg slightly older than that shown in Figure 1; the polar cell is formed and is embedded in the egg; the cleavage nucleus, preceded by the deep aster of the maturation spindle, is moving from the place of polar-cell formation toward the interior of the egg.

Fig. 3. First cleavage spindle, early stage.

Fig. 4. Longitudinal section (actual). The two nuclei formed at the first cleavage are separating; the notch and the granules at the periphery indicate the beginning of the formation of the first cleavage plane. The aster in the anterior (upper) end of the egg has divided, while the opposite aster is still entire.

Fig. 5. Two-cell stage seen from the dorsal side; the anterior end above. There are two asters in the cell $\overline{AB}^2$, while the aster in $\overline{CD}^2$ is still undivided.

Fig. 6. Two-cell stage, from the dorsal side; spindles in both blastomeres.

Fig. 7. View of an eight-cell stage; optical section through the quadrants B and D, showing the distribution of the yolk granules. Observe the concentration of granules in the ventral part of $d^{4\cdot 1}$, and the position of the asters in $d^{4\cdot 1}$ and $d^{4\cdot 2}$.

1

2

3

4

5

6

7

PLATE 2.

Fig. 8. Four-cell stage, viewed as a transparent object from the animal pole. The anterior end is above.

Fig. 9. Four-cell stage, later than Figure 8, seen from the right side. Spindles in C^3 and D^3; spherical nucleus in B^3.

Fig. 10. Four-cell stage, optical section through the cells B^3 and D^3, showing the division of the asters in preparation for the third cleavage.

Fig. 11. Five-cell stage, from the ventral side. The anterior end is above. The aster in $d^{4 \cdot 1}$ has divided laterally, the two parts being still connected. Spindles in A^3, B^3, and C^3 seen endwise.

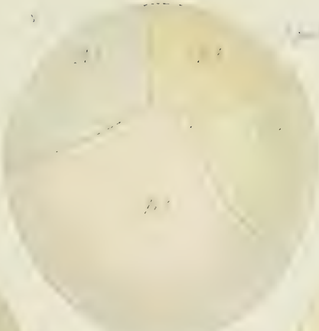
Fig. 12. Optical section, approximately sagittal, through the quadrants B and D, from the egg shown in Figure 11.

Fig. 13. Oblique view of the eight-cell stage, shortly after the third cleavage. The animal pole is marked by the polar cell; the anterior median line by the boundary between quadrants A and B.

Fig. 14. Dorsal view of the egg represented in Figure 13, showing the oblique position of the asters in $d^{4 \cdot 2}$, and the lateral extension of the aster in $c^{4 \cdot 2}$.

Fig. 15. Ventral view of the egg seen in Figures 13 and 14, showing the oblique position of the asters in $d^{4 \cdot 1}$, and the lateral extension of the aster in $c^{4 \cdot 1}$.

Fig. 16. Optical, nearly sagittal, section of the eight-cell stage, through the quadrants B and D, showing the dorso-ventral direction of the spindles in $d^{4 \cdot 1}$ and $d^{4 \cdot 2}$. Notice also the change of form of the quadrant B, as compared with the same quadrant in Figures 10 and 12.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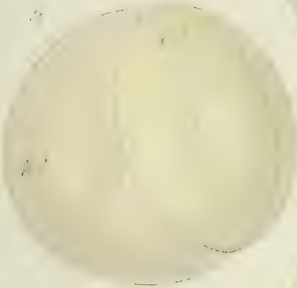
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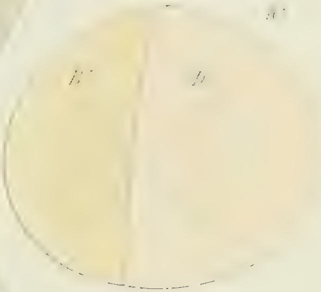
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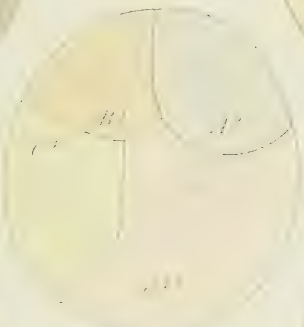
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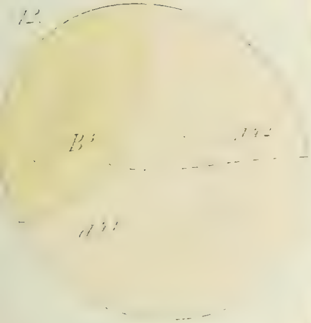
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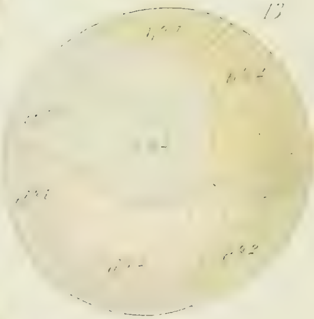
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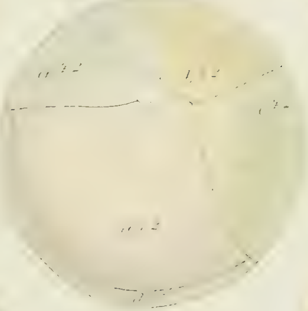
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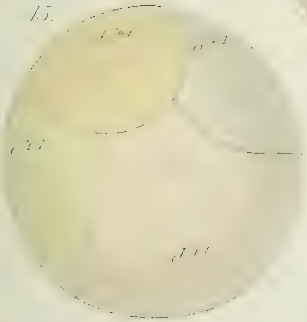
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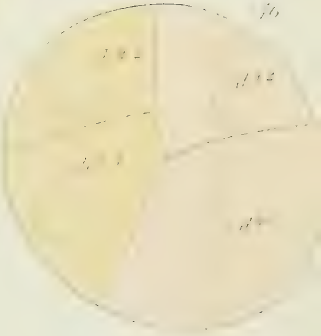
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B. Meisel lith. Boston.

PLATE 3.

Fig. 17. Right side of the eight-cell stage, same egg as that seen in Figures 13, 14, and 15, showing the lateral extension and beginning of division of the asters in $c^{4.1}$ and $c^{4.2}$.

Fig. 18. Right side of a slightly older stage than Figure 17, showing the completion of the division of the asters. In $c^{4.1}$ the line joining the asters is lateral; in $c^{4.2}$ it has already become oblique.

Fig. 19. Right side of a stage later than that shown in Figure 18, containing nine cells. The line joining the asters in $c^{4.2}$ has become dorso-ventral, while that joining those of $c^{4.1}$ has become oblique. The cleavage of $d^{4.1}$ into $d^{5.1}$ and $d^{5.2}$ has occurred (compare Fig. 16), while $d^{4.2}$ is still undivided.

Figs. 20–25. Different views of an egg in the ten-cell stage, to show the position of the spindles in relation to the exact form and dimensions of the cells.

Fig. 20. Right side of a stage later than Figure 19, but containing still only ten cells. The line joining the asters in $c^{4.1}$ has become dorso-ventral and the spindle is formed between them. Likewise in $c^{4.2}$; $d^{4.2}$ has divided into $d^{5.3}$ and $d^{5.4}$.

Fig. 21. Anterior surface of the egg represented in Figure 20; the spindles occupy the shorter axes of $b^{4.1}$ and $b^{4.2}$.

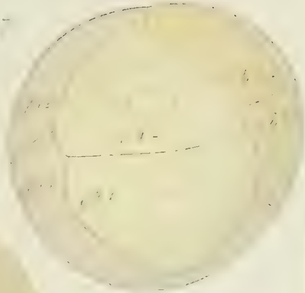
Fig. 22. Left side of same egg showing the nuclear conditions in quadrant *A*. The spindles are not yet formed.

Fig. 23. Right face of optical, nearly sagittal, section, through quadrants *B* and *D*, from the egg shown in the three preceding figures, to exhibit the exact dorso-ventral extent of the cells $b^{4.1}$ and $b^{4.2}$, as compared with the lateral extent of the same cells in Figure 21.

Fig. 24. Dorso-ventral, approximately frontal, optical section of the egg shown in Figures 20–23, showing the greatest dorso-ventral extent of the cells of quadrants *A* and *C*, for comparison with the lateral dimensions of the same cells, shown in Figures 20 and 22.

Fig. 25. Posterior surface (quadrant *D*) of the egg shown in Figures 20–24.

17.



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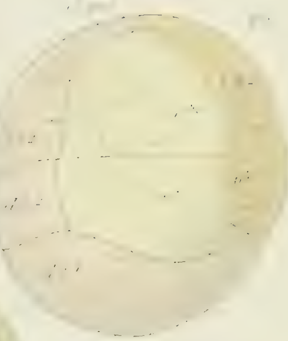

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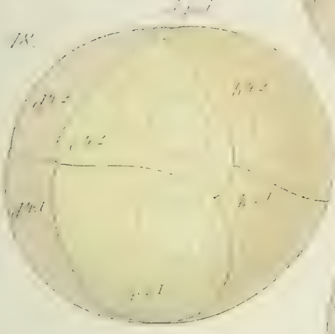
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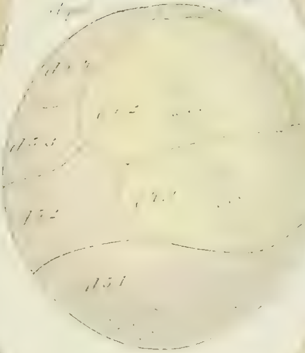
b 5.2
d 4.1
b 5.1
d 5.1

20.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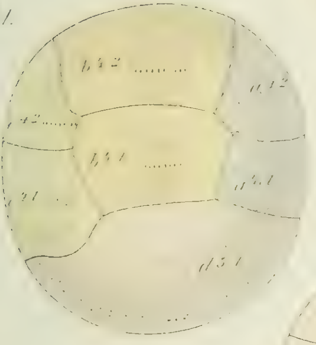
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d 4.2
b 5.1
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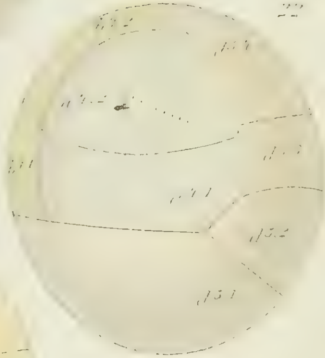
22.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d 4.1
d 5.2
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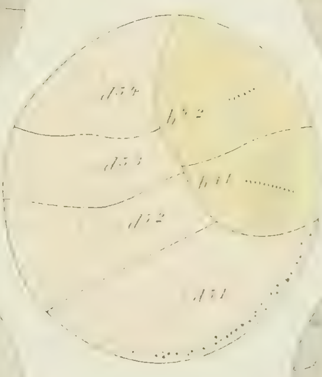
23.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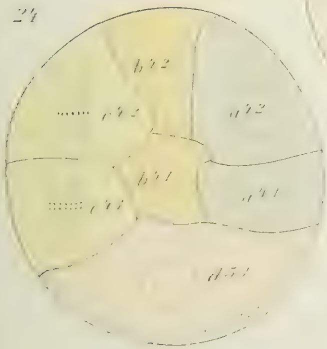
24.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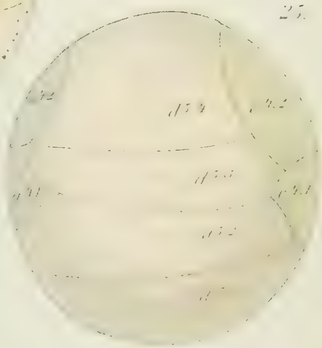
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B. Meisel Lith. Boston.

PLATE 4.

Figs. 26–29. Ten-cell stage.

Fig. 26. Left side of an egg in a ten-cell stage, slightly older than that shown in Figures 20–25. Note the dorso-ventral elongation of the cells $a^{4.1}$ and $a^{4.2}$, as compared with the same cells in Figure 22.

Fig. 27. Right side of the egg shown in Figure 26. The cytoplasm is beginning to become constricted in the cells of quadrant *C*.

Fig. 28. Dorso-ventral, approximately frontal, optical section of the egg shown in the two preceding figures, viewed from the anterior side, to show the greatest dorso-ventral extent of the quadrants *A* and *C* at this stage.

Fig. 29. Right side of the egg of Asplanchna *priodonta* Gosse, in the ten-cell stage, showing the spindles in the shorter axes of the cells.

Figs. 30–36. Sixteen-cell stage.

Fig. 30. Resting condition, seen from the anterior side.

Fig. 31. Left posterior view of the egg seen in Figure 30, showing the position of the asters in all the cells of quadrant *D*.

Fig. 32. Dorso-ventral, nearly sagittal, optical section through the quadrants *B* and *D*, from the egg shown in the two preceding figures.

Fig. 33. Posterior view of an egg slightly older than that shown in Figures 30–32.

Fig. 34. Nearly sagittal optical section, through the quadrants *B* and *D*, in the same stage as that shown in Figure 33.

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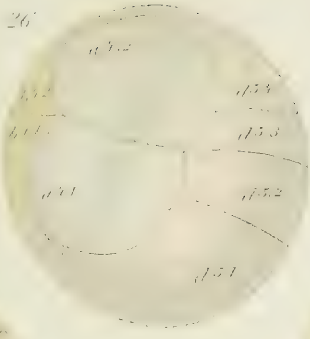
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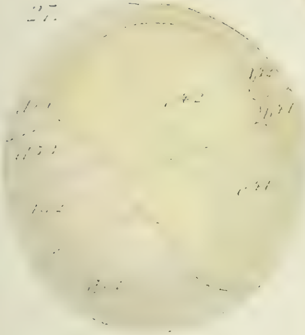

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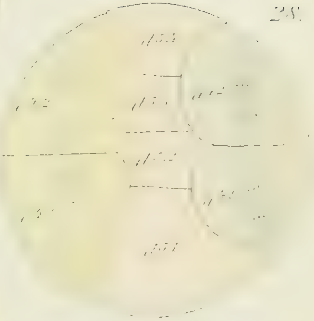

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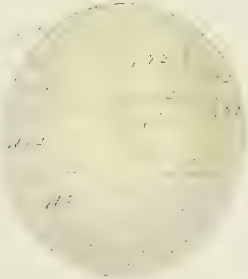

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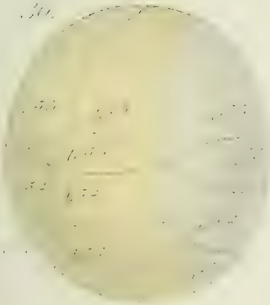

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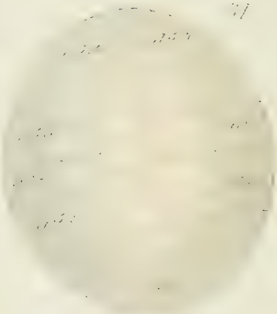

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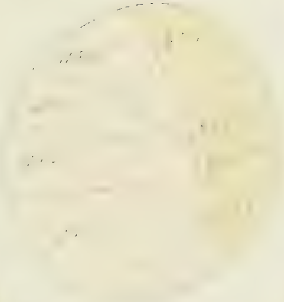

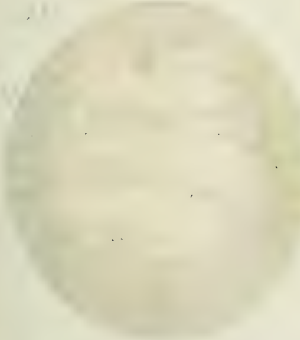

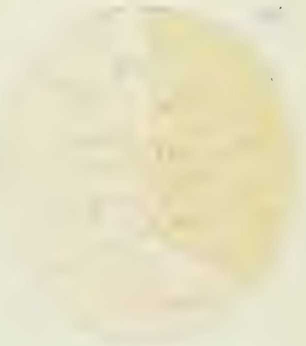

B. Meisel lith. Boston.

PLATE 5.

Fig. 35. Ventral view of a stage similar to that seen in Figures 33 and 34, Plate **4**, showing the antero-posterior position of the spindle in $d^{5 \cdot 1}$.

Fig. 36. Transverse optical section of the sixteen-cell stage, through the cells of the third layer, exhibiting the position of the spindle in $d^{5 \cdot 3}$. The section is viewed from the dorsal side. (Compare Plate **2**, Fig. 8.)

Figs. 37–42. Twenty-cell stage.

Fig. 37. Completion of the fifth cleavage in quadrant *D*. Note the oblique position of the elongated aster in $d^{6 \cdot 3}$.

Fig. 38. Sagittal optical section of the egg shown in Figure 37. The section passes, on the anterior side, between the cells of quadrants *A* and *B*, showing the cells of quadrant *A*.

Figs. 39–42. Different views of one and the same egg.

Fig. 39. Left side, showing the asters and spindles for the fifth cleavage in quadrants *A* and *B*.

Fig. 40. Right side of the egg shown in Figure 39. Observe the more advanced karyokinetic stages in quadrant *C*, as compared with quadrant *A*, Figure 39.

Fig. 41. View looking down upon the animal pole.

Fig. 42. View of the same egg from the ventral pole, showing the oblique position of the asters in $d^{6 \cdot 1}$.

Fig. 43. An older stage than that given in Figures 39–42; the fifth cleavage in progress; the egg contains twenty-seven cells. The cells $c^{5 \cdot 3}$ and $b^{5 \cdot 3}$ are forced apart by the cell $c^{6 \cdot 7}$.

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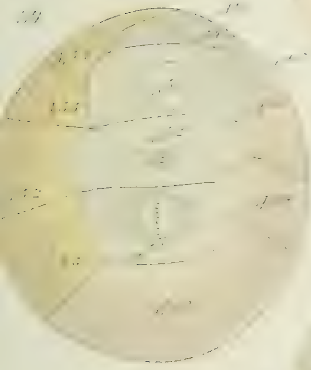


41.

PLATE 6.

Fig. 44. Right side of the egg shown in Figure 43, Plate **5**, 27-cell stage.

Fig. 45. Dorsal pole of the egg shown in Figures 43 and 44.

Fig. 46. Posterior view of the egg shown in the three preceding figures. Note the lateral position of the asters in $d^{6\cdot3}$.

Fig. 47. Right anterior surface of an egg, showing the quadrants *B* and *C* in the sixth generation.

Fig. 48. Sagittal optical section of the 32-cell stage, viewed from the right side, and showing the spindles in $d^{6\cdot1}$ and $d^{6\cdot3}$.

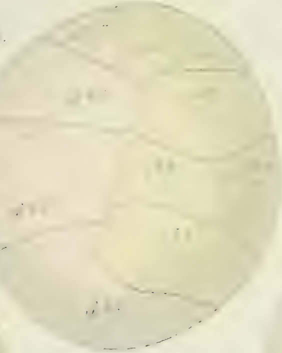
Fig. 49. Sagittal optical section of an egg slightly older than that seen in Figure 49, showing the process by which the cell $d^{7\cdot2}$ is formed at the sixth cleavage of the entoderm.

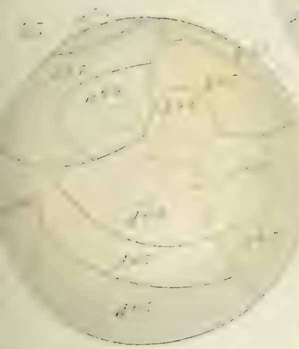
Fig. 50. Sagittal optical section of an egg a little older than that seen in Figure 49, showing the recently divided and separating asters in $d^{7\cdot1}$, and the beginning of migration of the cloud of granules which lies at the anterior ventral margin of the cell $d^{7\cdot1}$.

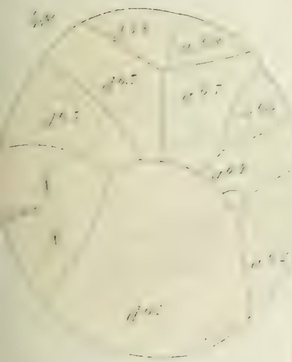
Fig. 51. Sagittal optical section of about the same stage as that shown in Figure 50. The nucleus of $d^{7\cdot1}$ has moved away from the periphery of the cell, and the cloud of granules is distributed between it and the small cells $d^{6\cdot2}$ and $d^{7\cdot2}$.

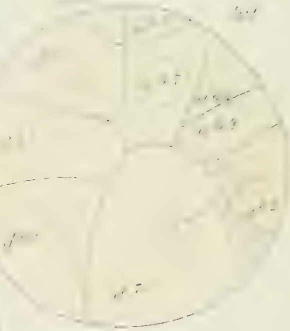
Apparently there is some slight variation in regard to the changes in the entoderm cell as compared with the other cells. From the condition of the remaining cells of the *D* quadrant, one would infer that Figure 51 is younger than Figure 50, though the migration of the cloud of granules is more advanced.

Fig. 52. Transverse optical section of the egg shown in Figure 51, through the region marked in Figure 51 by the cell $d^{6\cdot2}$. The section is viewed from the ventral side.









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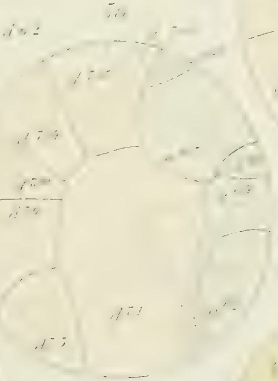

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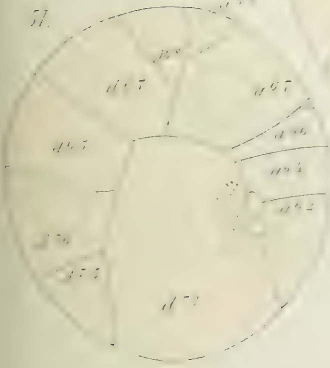

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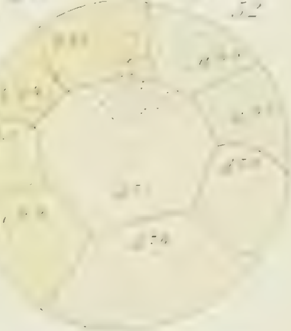


PLATE 7.

Fig. 53. Quadrant *D* at a stage a little older than that shown in Plate 6, Figure 46. The rotation of the asters in the cell $d^{6\cdot 3}$ is in progress. Thirty-two cells.

Fig. 54. Later stage than Figure 53, showing the final dorso-ventral direction of the spindle in $d^{6\cdot 3}$. A section of this egg is represented in Plate 6, Figure 48. Thirty-two cells.

Fig. 55. Anterior surface of 49-cell stage, showing the sixth cleavage in progress.

Fig. 56. Ventral end of the egg seen in Figure 55, showing the large cell $d^{7\cdot 1}$ nearly enclosed by the other cells.

Fig. 57. The sixth cleavage in quadrant *D*. 38-cell stage.

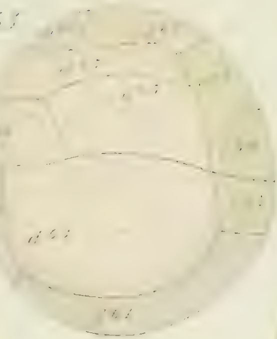
Fig. 58. Completion of the sixth and beginning of the seventh cleavage in quadrant *D*. Same egg as that shown in Figures 55 and 56.

Fig. 59. Dorsal view of the egg seen in Figure 57.

Fig. 60. Dorsal view of a stage later than the preceding, representing the same egg as that shown in Figure 58. Sixth cleavage nearly completed.

Fig. 61. Anterior view, showing the completion of the sixth cleavage in the quadrants *A* and *B* in all the cells except $a^{6\cdot 5}$. Sixty-nine cells.

53.



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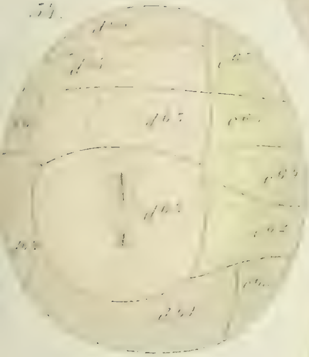

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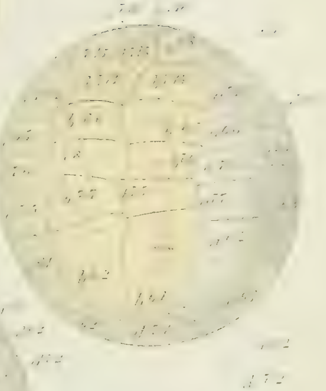

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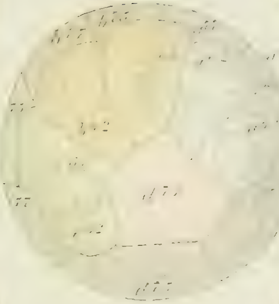

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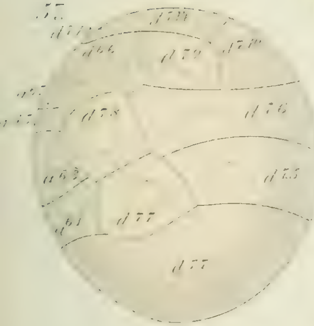

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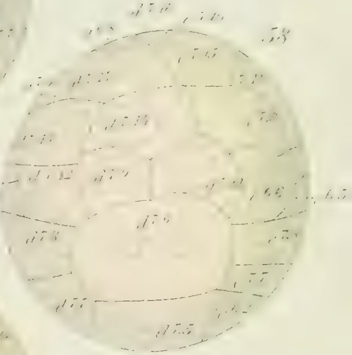

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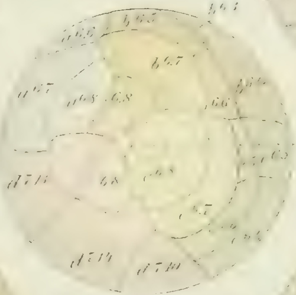

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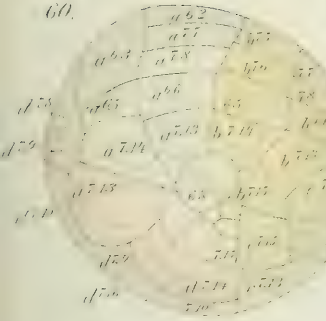

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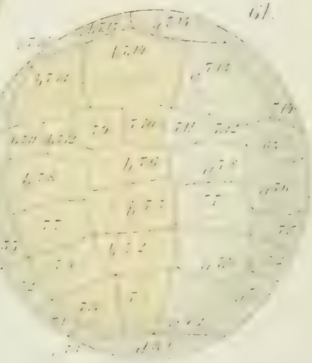

PLATE **8**.

Fig. 62. Dorsal view of an egg in approximately the same stage as that of Plate **7**, Figure 61. The four small unlabelled cells at the point of meeting of the four quadrants are $a^{7\cdot16}-d^{7\cdot16}$. About 69-cell stage.

Fig. 63. Ventral view of the egg shown in Figure 61, exhibiting the nearly complete enclosure of the entoderm (to which the cell $d^{8\cdot1}$ belongs) by the ectoderm.

Fig. 64. Sagittal optical section of the egg represented in Plate **7**, Figures 55, 56, and 59. The cloud of granules in the entoderm cell $d^{7\cdot1}$ now surrounds the dorsal aster of the spindle of the seventh cleavage.

Fig. 65. Sagittal optical section of the egg represented in Figures 61 and 63, showing the completed seventh cleavage in the entoderm; the cloud of granules forms a ring around the nucleus in the smaller entoderm cell $d^{8\cdot2}$. The ring being cut twice, appears in the form of two groups of granules, one anterior, the other posterior to the nucleus.

Fig. 66. Posterior view, showing the seventh cleavage in quadrant *D*.

Fig. 67. Left posterior view; the seventh cleavage nearly finished in quadrant *D*; the sixth not yet finished in quadrant *A*. From the egg represented in Figures 61, 63, and 65. Sixty-nine cells.

Fig. 68. Posterior view of a later stage than that represented in Figure 67. The line separating $d^{8\cdot11}$ and $d^{8\cdot12}$ is the posterior median line; the spindles are seen to be arranged symmetrically with respect to this line, so that the cleavage is becoming bilateral. The entoderm is entirely covered by the ectoderm; the region where $a^{7\cdot1}$ and $d^{8\cdot9}$ are in contact shows the place where the entoderm cells formerly occupied the surface. 82-cell stage.

Figs. 69–74 give different views of the same egg, a 94-cell stage.

Fig. 69. Anterior surface, showing the finished meridional cleavage forming the cells $a^{8\cdot11}-c^{8\cdot11}$, $a^{8\cdot12}-c^{8\cdot12}$, $a^{8\cdot15}-c^{8\cdot15}$, and $a^{8\cdot16}-c^{8\cdot16}$, and the spindles for the equatorial cleavage of $a^{7\cdot5}-c^{7\cdot5}$ and $a^{7\cdot7}-c^{7\cdot7}$.

Fig. 70. Right side of the egg shown in Figure 69.

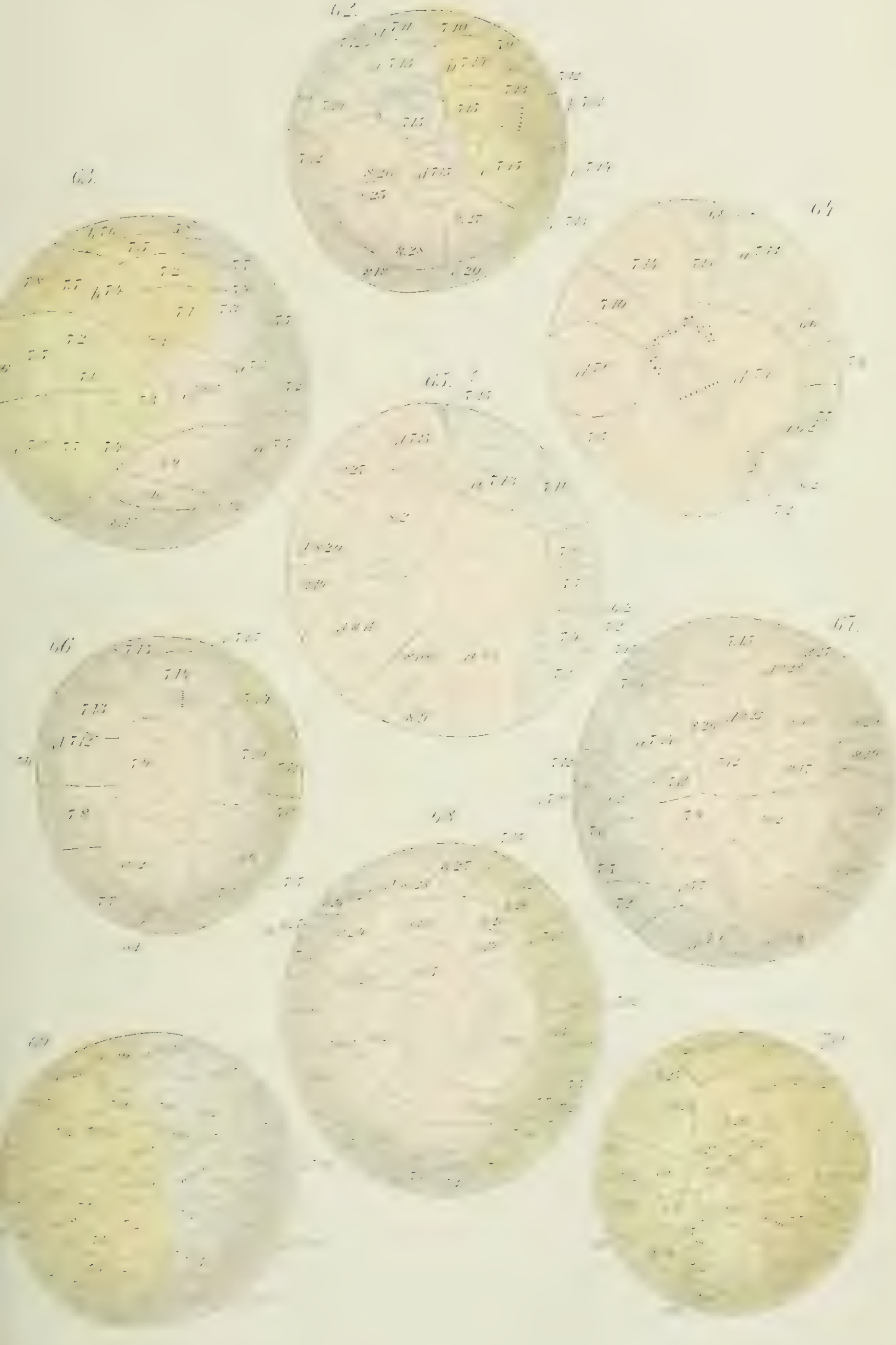
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PLATE 9.

Fig. 71. Left side of the egg shown in Figures 69–74. Ninety-four cells.

Fig. 72. Dorsal view of the egg represented in Figures 69–74. The small cells in the centre, at the point of meeting of the four quadrants, are $a^{7\cdot16}-d^{7\cdot16}$.

Fig. 73. Ventral end of the same egg, showing the crowding together of the cells of the quadrants *A*, *B*, and *C* in this region.

Fig. 74. Posterior view of the same egg, showing spindles for the ninth cleavage in some of the cells of quadrant *D*, and the ninth cleavage completed in other cells of that quadrant.

Fig. 75. Anterior surface of a later stage, containing about 120 cells. At the ventral end (lower part of the figure) the cells are much crowded and many of them are very small. The vesicles immediately below the cells $b^{8\cdot15}$, $a^{8\cdot10}$, and $a^{8\cdot11}$ are the small ventral products of the cleavage of $a^{7\cdot5}-c^{7\cdot5}$ and $a^{7\cdot7}-c^{7\cdot7}$, the spindles for which are shown in Figures 69 and 70, Plate **8**.

Figs. 76–79. Successive stages in which the ectoderm is conceived to have been removed from the right side, to show the entoderm cells.

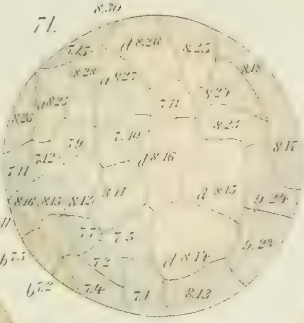
Fig. 76. Egg at the stage shown in Figure 75. A frontal section of this egg is given in Plate **10**, Figure 81.

Fig. 77. Slightly older stage than Figure 76, viewed in the same way.

Fig. 78. Slightly older stage than Figure 77, showing the change in the position of the cells of the entoderm and of those at the animal pole. A view of this egg from the animal pole is shown in Plate **10**, Figure 82.

Fig. 79. Later stage than Figure 78. The entoderm cells have changed position still further, and are approaching cleavage.

71.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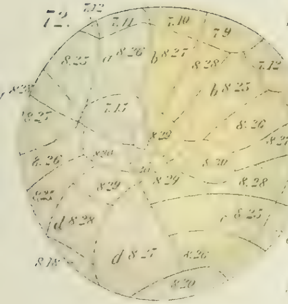
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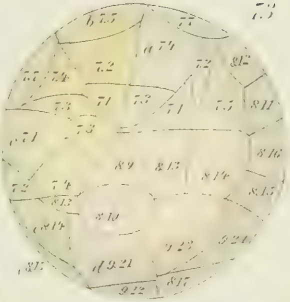
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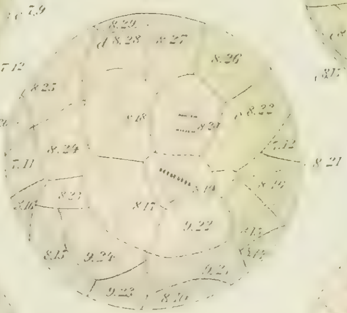
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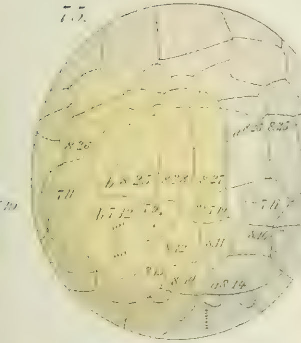
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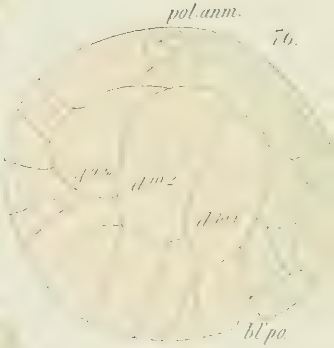
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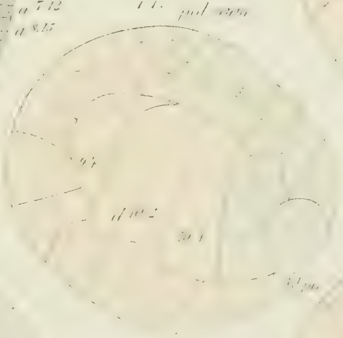
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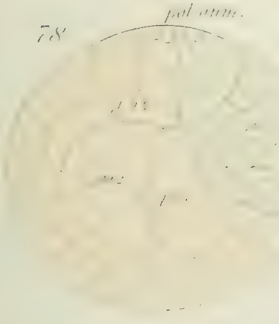

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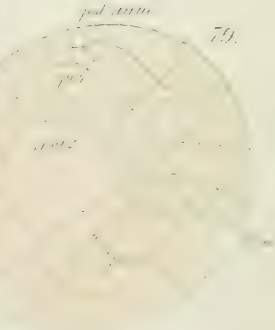


PLATE 10.

Fig. 80. Optical section (approximately frontal) of an egg in the stage seen in Figures 69–74, showing the very unequal division of $d^{8 \cdot 2}$.

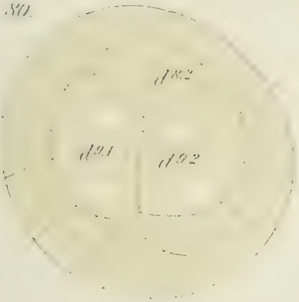
Fig. 81. Optical section (approximately frontal) of a stage later than Figure 80, showing the five large entoderm cells. A side view of the same egg is seen in Plate 9, Figure 76.

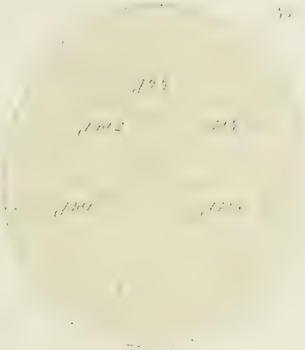
Fig. 82. Stage slightly later than that of Figure 81. The ectoderm is supposed to have been removed from the dorso-anterior part of the egg, disclosing the position of the entoderm cells. A side view of the same egg is shown in Plate 9, Figure 78.

Fig. 83. Later stage than the preceding, viewed in the same manner. A spindle has appeared in each of the five large entoderm cells.

Fig. 84. Optical sagittal section of an embryo at about the time of the beginning of the formation of organs.

80.





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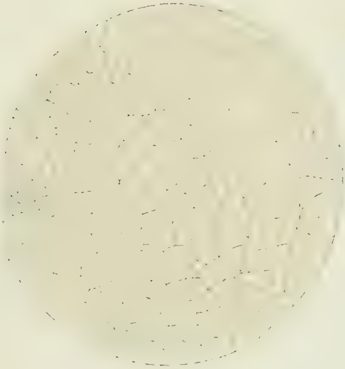

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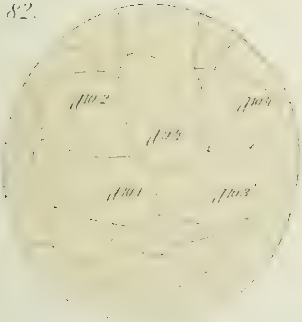
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No. 2. — *Studies from the Newport Marine Laboratory.* Communicated by ALEXANDER AGASSIZ.

XL.

Some Variations in the Genus Eucope. BY ALEXANDER AGASSIZ AND W. McM. WOODWORTH.

WE examined for various points nearly four thousand specimens of Eucope (3,917).

Among these we found nine specimens with only three radial canals, twenty with five, and three with six radial canals.

There were fourteen specimens in which one of the radiating canals forked, the forking distal or proximal to the genitals being nearly equally divided.

No less than thirty-nine specimens showed distinct traces of serrations or spurs from one or more of the radial canals.

In eight specimens the radial serrations or spurs were not well defined, and the position and number of the radial canals were indistinct.

In eight specimens marginal tentacles were observed, which had become united at the circular canal, sometimes with the tentacle next to the tentacle with the otolith.

In six specimens there were marked spurs projecting from the base of some of the marginal tentacles.

In eight specimens there were two otoliths in each sense capsule. In four there were three.

In the other specimens the principal variations extended only to the degree of development of the cycles of the marginal tentacles and of the genital organs. The latter showed in some cases peculiar leaf-like expansions extending laterally from the radial canals.

The radial canals were four in number in an overwhelming majority of the specimens examined.

The study of some of the variations in the genus Eucope was undertaken with a view of calling attention to the changes undergone in a species of jellyfish, of which great numbers are always easily obtained during the summer months. The size of the full grown Eucope is so small that with an ordinary hand lens striking variations can at once be detected, and it is possible with a low power to pass in review with comparative ease a large number of specimens.

We hope also to call the attention of zoölogists to the advantages of photography, not only in an investigation of this kind, but also to its application for ordinary purposes of delineation. (See Plate VI. Figs. 3–6.)

Dr. Woodworth photographed the specimens reproduced here on Plates I.–VI., and he has written a short account of the methods he followed.

In reviewing the variations we have observed in one species of Eucope (E. diaphana), we may call attention to the similarity of these variations which occur in this simple Medusa to structures found sometimes in closely allied genera or families, and even in some cases to characters of groups considered as only distantly related to the genus we have examined.

The great number of marginal tentacles in Eucope they have in common with the Æquoridæ.

Eucope shares with the Oceanidæ the limited number of marginal tentacles connected with sense organs. Pendant leaf-like expansions of the genital organs recall those of Melicertidæ.

The presence in Eucope of spurs at the base of the marginal tentacles recalls similar structures in Zygodactyla, Halopsis, and the like.

The forking or branching of the radial canals below the genitals is found also in Willia and in the Berenicidæ, a family allied to the Æquoridæ; the forking is symmetrical in the latter, and asymmetrical in the former genus.

The increase in number of the radial canals from the pouch at the base of the manubrium is a structural feature which is characteristic of the Æquoridæ.

The serration of the radial canals is a generic character of Saphenia and allied genera.

The branching or sending off spurs from the radial canals of Eucope is a structural feature found in Gonionemus, Ptychogena, Polyorchis, and allied forms. The lateral offshoots in Polyorchis being, however, arranged in regular succession on each side of the radial canal, much like the rounds of a ladder.

The anastomosing of the radial canals is a feature now characteristic of the Discophores.

In the increase and special arrangement of the otoliths in the sense organ of Eucope we find the first trace of the specialization of the sense organs of such genera as Oceania, Tiaropsis, and the like.

There were no variations noted in the shape of the digestive cavity, or in the number of actinal lobes of the manubrium,[1] even in specimens with five or six radial canals in place of the normal number (four) o radial canals. The actinal folds were always found to be four in number. In one case only have we found the radiating canal originating from the circular canal. (Plate VIII. Fig. 19.)

The origin of the peculiar club-shaped intertentacular appendages characteristic of Halopsis and Laodicea, as well as the spur at the base of the tentacles in many Æquoridæ, may be referred to the spur-like appendages of the marginal tentacles of Eucope figured in Plate VIII. Figs. 4–13.

And it may not be far out of the way to look upon the coalescence of adjoining marginal tentacles with sense organs as the first indication of such structural features as the radial marginal tentacles of Eucheilota, or even of Boungainvillia, Margelis, or Nemopsis.

It is interesting to note that in Echinoderms there are five radial canals, and four or six or more are considered monstrosities, while in Acalephs four or its multiples are the normal number of radial canals, and five or less are variations.

The specimens of Eucope showing numerical or structural variations were as a rule fully developed males or females, the eggs and spermatozoa being apparently in a healthy condition.

It would be an interesting study in heredity were it possible to breed the variations in Eucope here enumerated, and ascertain how far the structural characters acquired in the variations we have observed can be transmitted, and lead perhaps finally to the formation of types which we have been accustomed to look upon as having no structural relation with the genus.

But it is also possible that in a comparatively simple genus like Eucope these variations are not necessarily to be considered as hereditary; they may indicate possibilities in mechanical combinations which have become characteristic of jellyfishes, and result from their mode of life and the simplicity of their structure. Their repetition in closely allied genera may denote structural affinity, while in distantly allied groups it may be the result of mechanical combinations, and in no way indicate any affinity.

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[1] Variations in the manubrium have been observed in Tubularian Hydroids, such as Lizzia, Dysmorphosa, Hybocodon, Dipurena, and Sarsia; but as they are usually connected with phenomena of reproduction and of budding they have only a distant connection with the line of the present investigation. See an interesting paper by Hartlaub on the reproduction of the manubrium of Sarsia, in Verhandl. d. Deutschen Zool. Gesell., 1896.

The four primary segments of Eucope are of uniform size in the majority of the specimens examined. Whenever there is suppression of a radial canal, as in the case of specimens with three radial canals, the segments are sometimes uniform (Plate III. Figs. 3, 6), or one of the segments, as in Plate III. Fig. 1, is nearly 180°, indicating the total suppression of the fourth radial canal at its normal point of development. See also Plate III. Fig. 4, in which one of the segments is smaller than the two from which the fourth section has been cut.

The inequalities which exist in the segments of some of the specimens can best be expressed by a table: —

$$1;\ 1;\ 1; - \frac{2}{1};\ 1;\ 1; - 1;\ \frac{3}{1};\ \frac{3}{1}; - 1;\ \frac{6}{1};\ \frac{2.5}{1};$$

$$1;\ 1;\ 1;\ 1; - 1;\ \frac{5}{1};\ 1;\ \frac{5}{1}; - 1;\ \frac{3}{1};\ 1;\ \frac{3}{1}; - 1;\ \frac{4}{1};\ 1;\ \frac{4}{1}; - 1;\ \frac{2}{1};\ \frac{3}{1};\ \frac{3}{1}$$

$$1;\ 1;\ 1;\ 1;\ 1; - \overbrace{1;\ \frac{2}{1}};\ \frac{3}{1};\ \frac{3}{1};\ \frac{3}{1}; - \overbrace{1;\ 1};\ 1;\ 1;\ 1;$$

$$\overbrace{1;\ \frac{1.5}{1}};\ \frac{2.5}{1};\ \frac{2.5}{1};\ \frac{2.5}{1}; - \overbrace{1;\ \frac{2.5}{1}};\ \frac{3.5}{1};\ \frac{3.5}{1};\ \frac{3.5}{1}; - \overbrace{1;\ \frac{3.5}{1}};\ \frac{4}{1};\ \frac{4}{1};\ \frac{3.5}{1};$$

$$\overbrace{1;\ 1};\ \frac{2}{1};\ \frac{2}{1};\ \frac{2}{1}; - 1;\ \frac{2}{1};\ 1;\ 1;\ \frac{2}{1};$$

The $\overbrace{\quad}$ indicates a fork of the radial canal.

$$1;\ \frac{2.5}{1};\ 1;\ \frac{2}{1};\ \frac{2}{1};\ \frac{2}{1}; - 1;\ \frac{2}{1};\ 1;\ \frac{1.5}{1};\ \frac{2}{1};\ \frac{1.5}{1}; - 1;\ \frac{1.5}{1};\ \frac{2}{1};\ \frac{2}{1};\ \frac{2}{1};\ \frac{2}{1};$$

$$1;\ \frac{1.5}{1};\ \frac{1.5}{1};\ \frac{1.7}{1};\ \frac{1.5}{1};\ \frac{1.5}{1};$$

In this table 1 expresses the smallest segment; the approximate dimensions of the others are represented by multiples of it thus: $\frac{2}{1}$ indicates that a segment is twice as wide at the periphery as the smallest; $\frac{3.5}{1}$, that it is three and a half times as wide. Of course, the value of 1 is a different value in each case.

1; 1; 1; is the formula for the segments of a Eucope in which they are of equal size, the radial canals forming an angle of 120° at the centre.

1; 1; 1; 1; and 1; 1; 1; 1; 1; would each denote the formula for segments of equal dimensions in a Eucope with four and one with five segments.

The formation of additional radial tubes may be due to the growth of independent tubes from the pouch at the base of the digestive cavity, or from the forking of tubes, the new canals eventually reaching the marginal canal. In one case we observed a radial canal which had its origin at the periphery and did not extend to the base of the manubrium (Plate VIII. Fig. 19). Such a formation of a new radial canal from the circular canal suggests a similar structure in the short canals, in which are found clusters of lasso cells extending at right angles from the periphery between the primary radial canals of Willia, and perhaps other Medusæ, in which we have clusters of lasso cells extending a short distance on the outer surface of the umbrella from the marginal canal.

In the great majority of the specimens of Eucope observed, the radial canals are tubes with walls nearly parallel all the way from the base of the digestive cavity to the marginal canal (Plates I.–VI.). But in a great many instances this parallellism does not exist, and we find on the edge of some of the radial canals slight serrations, as in Plate VII. Figs. 1–4 and 6. These serrations vary greatly in size, and in some cases become short spurs (Plate II. Fig. 4, Plate III. Fig. 3, Plate VII. Figs. 2, 3, 5, 7), or even spurs of considerable length (Plate VII. Figs. 6, 9, 10); the longer spurs becoming often the forks of the primary radial canals (Plate III. Figs. 1, 2–5, Plate VI. Figs. 1, 2, Plate VII. Fig. 5), either above or below the genital pouches. Or the spurs may form connecting canals between the radial tubes (Plate VII. Fig. 4, Plate VIII. Fig. 20), or a rudimentary circular canal round the base of the manubrium (Plate VII. Fig. 8).

Starting with the normal state, in which the genitals are equally developed, we find five or six variations, which cover by far the greater number of the specimens examined.

The greatest number of the specimens (622 out of 1146) examined for variations in the genital organs were normal, the four genitals being equally developed; the females were more numerous than the males; of the latter there were 175, and of the former 447. This stage is represented in the table by 1; 1; 1; 1; in which 1 means that the genitals are fully developed, and equally so on each radial canal, of which there are four.

The next stage represented by the formula, 1 ; 1 ; 1 ; 0 ; the genitals were atrophied on one of the radial canals and equally developed on the others. Seventy-eight specimens of this stage, 49 females and 29 males.

The next most frequent stage is that in which two adjoining genitals are fully developed ; the others are of the same size, but less well developed ; that stage is represented by the formula 1 ; 1 ; 2 ; 2 ; Out of the 1,146 specimens examined there were only 74 specimens of this stage, of which 45 were females and 29 males.

Next comes the stage in which only one of the genitals is fully developed ; the others are less so, corresponding to the formula 1 ; 2 ; 2 ; 2 ; 39 females and 27 males.

In the order of frequency of occurrence comes :

Eucope with the formula 1 ; 1 ; 1 ; 2 ; — 28 females and 17 males.

Then comes the stage in which the genitals were unequally developed : 20 females and 21 males.

Next,

Eucope with the formula 1 ; 0 ; 0 ; 0 ; — 24 females and 13 males.
“ “ “ 1 ; 2 ; 0 ; 0 ; — 15 “ “ 3 “
“ “ “ 1 ; 2 ; 2 ; 0 ; — 10 “ “ 8 “

In specimens with three radial canals we observed only one specimen in which the genitals were uniformly developed. On Plate III. are seen (Fig. 1) a specimen in which one of the canals forks at the extremities of the heart-shaped genitals, forming three primary segments of nearly equal size extending to the centre of the disk, with a small sector cut from the outer edge of two adjoining segments.

Figure 4 of the same plate shows a specimen with three radial canals and four genital pouches, but the canal which forks subdivides above the genitals so near the centre of the disk as to subdivide the disk into four nearly equal segments.

A variation similar to that of Plate III. Fig. 1, for a three-rayed Eucope, has been observed in a four-rayed Eucope (Plate III. Fig. 2), in which the fifth sector is a comparatively small triangle cut out from the periphery of two of the adjoining sections, extending to the centre of the disk.

In Figure 5 of Plate III. the forking of the four-rayed Eucope, taking place nearer the centre of the disk, subdivides the disk into segments of more uniform size, and it closely resembles a five-rayed Eucope.

In five-rayed Eucope only one specimen was observed with equally developed genitals (Plate V. Fig. 1). Those figured on Plate VI., as well as the others on Plates IV. and V., all show a very great range of variation in their development. In two cases (Plate IV. Figs. 3, 6) two of the genitals are wanting.

In Plate VI., Figures 1 and 2 are those of two specimens with five radial canals, both of which fork so near the base of the manubrium as to divide the disk into six nearly equal segments.

The accompanying table will show the other variations which have been observed, and their frequency.

1146 SPECIMENS EXAMINED FOR VARIATIONS IN THE DEVELOPMENT OF THE GENITAL ORGANS ON EACH OF THE FOUR RADIAL CANALS.

With Three Radial Canals, or Three with Fork.

1; 2; 3;	3	females, and	1	male.
1; 1; $\underbrace{1; 1}$;	2	" "	1	"
1; 1; 1;	1	female.		
1; 1; 0;	2	"		

With Four Radial Canals.

1; 1; 1; 1;*	447	females and	175	males.
1; 1; 1; 0;	49	" "	29	"
1; 1; 2; 2;	45	" "	29	"
1; 2; 2; 2;	39	" "	27	"
1; 1; 1; 2;	28	" "	17	"
1; 2; 3; 4;	20	" "	21	"
1; 0; 0, 0;	24	" "	13	"
1; 1; 0; 0;	21	" "	9	"
1; 2; 3; 0;	19	" "	7	"
1; 2; 0; 0;	15	" "	3	"
1; 2; 2; 0;	10	" "	8	"
1; 1; 2; 0;	6	" "	8	"
1; 1; 2; 3;	5	" "	4	"
1; 2; 2; 3;	5	" "	4	"
1; 2; 3; 3;	4	" "	3	"
1; 0; 0; 2;	3	" "	2	"
1; 0; 2; 3;	3	" "	2	"
1; 1; 0; 2;			4	males.

* 1, fully developed genitals; 2, genital smaller than 1; 3, genital smaller than 2; 4, genital smaller than 3; 5, genital smaller than 4; 0, genital organ absent. The semicolon (;) indicates the position of the radial canal. The $\underbrace{\quad}$ indicates the forking of the radial canal.

1; 0; 2; 0;	4 females.
1; 2; 2; 3;	3 “
0; 0; 0; 0;	3 specimens.
1; 2; 0; 3;	2 females.
1; 2; 1; 3;	1 “
1; 2; 3; 1;	1 “
1; 1; 1; 4;	1 “
1; 0, 0; 1;	1 male.
1; 1; 1; 3;	1 female.
1; 0; 1; 0;	1 “
1; 1; 4; 4;	1 “
1; 3; 2; 0;	1 “
1; 2; 0; 4;	1 male.
1; 2; 1; 2;	1 female.
1; 2; 2; 4;	1 “
1; 0; 3; 4;	1 “

With Five Radial Canals, or Four and Five with Fork.

$1; \underbrace{2; 2}; 2; 0;$	1 female.
1; 2; 3; 4; 5;	2 females and 1 male.
1; 3; 0; 2; 0;	1 “
1; 2; 2; 3; 4;	1 male.
1; 3; 3; 4; 4;	1 female.
1; 2; 2; 2; 3;	1 “
1; 1; 3; 0; 4;	1 “
1; 1; 1; 1; 1;	1 male.
1; 3; 3; 3; 4;	1 “
1; 1; 3; 4; 4;	1 female.
2; 4; 2; 4; 5;	1 “
1; 2; 3; 0; 4;	1 male.
$1; 3; 3; \underbrace{4; 4};$	4 females and 1 male.
$1; 1; \underbrace{4; 4}; 2;$	3 females and 1 male.

The variations in the shape of the genitals from a circular to an elliptical outline to lobate, foliate, or elongate shape (Plate VIII. Fig. 21) is usually connected with the growing together of the genitals of adjoining radial canals (Plate VIII. Fig. 18) or with their separation into two distinct bodies when the radial canals fork (Plate III. Figs. 1, 5).

It will be seen that in Eucope, as has been observed in Aurelia, the tendency in the numerical variation of the genitals is greatest in the direction of an increase rather than a diminution in their number. A similar tendency is also noticed in the numerical variation of the radial canals of the otoliths.

The youngest specimens of Eucope observed (eleven in number) had twelve tentacles in all, one at the base of each of the four radial canals and two in each quadrant with a sense organ, and without any tentacles intermediate between the radial and the sense organ tentacle. It is possible that these specimens may belong to a different species, as the youngest specimens of Eucope diaphana I have raised from the hydroid already had 24 tentacles.[1] But of course it is possible that the above stage may have dropped from the reproductive calycle at an earlier stage of development.

Were the marginal tentacles to develop regularly we should have as the third stage a Eucope with 48 tentacles, a fourth stage with 96, and a fifth stage with 192.

But as far as our experience shows, we find normal Eucope only in the first and second stages, and even then there are numerous variations.

The formulæ for the normal stages are, calling T any marginal tentacle,

T_c, the primary tentacle at the base of the radial canals;

T_0, the primary tentacle with a sense organ at its base;

t_1, the first set of marginal tentacles appearing between T_c and T_0 in the stage with 24 marginal tentacles;

t_2, the second set of marginal tentacles on each side of t_1, in the stage with 48 marginal tentacles;

t_3, the third set of marginal tentacles on each side of t_2, in the stage with 96 marginal tentacles;

t_4, the fourth set of marginal tentacles on each side of t_3, in the stage with 192 marginal tentacles;

t_5, the fifth set of marginal tentacles on each side of t_4, in the next stage with as many (theoretical number 31 tentacles) as $16t_5$, $8t_4$, $4t_3$, $2t_2$, $1t_1$ tentacles between the (T_c and T_0) radial canal and sense organ tentacle, or 95 tentacles in each quadrant between the radial canals, or a total theoretical number of 384 marginal tentacles.

The formula of the youngest stage, or first stage, would be

$$\Sigma\ (4)\ T_c + (4)\ 2\ T_0 = 12\ T,$$

or two tentacles with a sense organ in each quadrant.

That of the second stage,

$$\Sigma\ (4)\ T_c + (4)\ 2\ T_0 + (4)\ 3t_1 = 24\ T,$$

or two tentacles with a sense organ in each quadrant with a tentacle of the t_1 order between each and the radial canal and sense organ.

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[1] Proc. Boston Soc. Nat. Hist., June 4, 1862, p. 92.

That of the third stage,

$$\Sigma\ (4)\ T_c + (4)\ 2\ T_0 + (4)\ 3t_1 + (4)\ 6t_2 = 48\ T,$$

the same as the second stage, with an additional tentacle of the t_2 order intercalated on each side of the t_1 tentacles, making 11 tentacles in each quadrant, or three between each of the three primary divisions of the quarter.

The fourth stage,

$$\Sigma\ (4)\ T_c + (4)\ 2\ T_0 + (4)\ 3t_1 + (4)\ 6t_2 + (4)\ 12t_3 = 96\ T,$$

or a tentacle of the third order, t_3, intercalated on each side of t_2, thus making 7 tentacles in each of the primary divisions of the quarter.

The fifth stage, with 192 tentacles, would have for its formula,

$$\Sigma\ (4)\ T_c + (4)\ 2\ T_0 + (4)\ 3t_1 + (4)\ 6t_2 + (4)\ 12t_3 + (4)\ 24t_4 = 192\ T,$$

or a tentacle of the fourth order, t_4, intercalated on each side of t_3, thus making 15 tentacles in each of the primary divisions of the quarter.

The theoretical formula for the sixth stage, with 384 tentacles, would be,

$$\Sigma\ (4)\ T_c + (4)\ 2\ T_0 + (4)\ 3t_1 + (4)\ 6t_2 + (4)\ 12t_3 + (4)\ 24t_4 + (4)\ 48t_5 = 384\ T,$$

a tentacle of the fifth order, t_5, having been intercalated on each side of the tentacles of the t_5 order, thus making 41 tentacles in each of the primary divisions of the quarter.

It is not necessary to carry these stages any further, as the largest number of tentacles observed in any primary division of each quadrant is not greater than thirteen, which would limit it to a modified stage of 192 marginal tentacles.

The accompanying tables have been arranged so as to indicate the association, whatever their number may be, with the highest number of marginal tentacles occurring in any primary quadrant. This number may be a normal number between any T_c and T_0, or between any T_0 and T_0, and may be due to the absence of one of the T_0 tentacles, or of both, in the quadrant.

A glance at the tables shows how few of the specimens examined possessed the normal number of tentacles. We should have as the normal stages of each quadrant for the four stages up to 192 tentacles.

T_c, T_0, T_0, T_c, first stage, with 12 marginal tentacles.

T_c, t_1, T_0, t_1, T_0, t_1, T_c, second stage, with 24 marginal tentacles; or, as in the tables, 1, 1, 1; 1, 1, 1; 1, 1, 1; 1, 1, 1; of which eleven specimens were seen from the number tabulated for numerical variations.

The formula for the third stage, with 48 tentacles, is,

$$T_c, t_2, t_1, t_2, T_0, t_2, t_1, t_2, T_0, t_2, t_1, t_2, T_c,$$

or, as in the table, 3, 3, 3; 3, 3, 3; 3, 3, 3; 3, 3, 3; of which fourteen specimens were found from the number tabulated for variations.

In the fourth stage the formula is,

$$T_c, t_3, t_2, t_3, t_1, t_3, t_2, t_3, T_0, t_3, t_2, t_3, t_1, t_3, t_2, t_3, T_0, t_3, t_2, t_3, t_1, t_3, t_2, t_3, T_c,$$

or 96 marginal tentacles.

Of this normal stage only two specimens were observed.

Of the fifth stage, with 192 marginal tentacles, of which the following is the formula, not a single normal stage was observed:

$$T_c, t_4, t_3, t_4, t_2, t_4, t_3, t_4, t_1, t_4, t_3, t_4, t_2, t_4, t_3, t_4, T_0, t_4, t_3, t_4, t_2, t_4, t_3, t_4, t_1, t_4, t_3, t_4, t_2, t_4, t_3, t_4, T_0, t_4, t_3, t_4, t_2, t_4, t_3, t_4, t_2, t_4, t_3, t_4, t_1, t_4, t_3, t_4, t_2, t_4, t_3, t_4, T_c.$$

But a few specimens were seen with the normal number of 15 tentacles in some of the primary divisions of one quadrant.

Of the sixth stage, with 41 tentacles in each of the primary divisions of the quadrant, not a single specimen was collected.

It is interesting to note that in the specimens which may be said to belong to the second stage, some of the primary divisions of the quadrants remain in the first stage with only one tentacle, and others with two, the third tentacle not having developed.

Between the second and third stage, in a number of specimens, the greatest number of tentacles in a primary division of the quadrant is four, and the smallest one. In a number of cases two or even three of the quadrants remain in the second stage, and only in one quadrant do we find four tentacles in a primary quadrantic division. Similarly, we find a number of specimens with five tentacles as the largest number in any primary quadrantic division, and some of the quadrants in the second stage, but none in the first. Even when we come to six tentacles as the largest number of tentacles in any primary quadrantic division, we still find some of the primary quadrantic divisions in the second stage, and occasionally a whole quadrant or a quadrantic division above the first stage, as is the case in the second stage and stages intermediate with the third.

Only four specimens typical of the normal third stage were observed, and the great majority of the other specimens in which seven tentacles were found in a quadrantic division belonged to stages approximating the third more nearly than the second. Only a small proportion of the specimens were observed in which the quadrantic divisions belonged to

With not more than six tentacles in any subdivision : —

5, 5, 6; 6, 5, 5; 6, 6, 5; 6, 5, 6;
6, 4, 3; 5, 5, 5; 5, 6, 3; 3, 6, 5;
3, 4, 4; 4, 4, 4; 3, 4, 5; 5, 6, 5;
4, 3, 3; 4, 5, 4; 5, 4, 4; 6, 3, 5;
5, 5, 5; 5, 4, 3; 6, 6, 4; 4, 4, 3;
4, 4, 4; 5, 4, 4; 5, 5, 5; 5, 6, 5;
4, 4, 4; 4, 4, 4; 3, 6, 2; 4, 6, 5;
3, 4, 4; 5, 4, 4; 3, 6, 3; 4, 6, 5;
3, 3, 5; 5, 6, 6; 4, 5, 6; 5, 3, 4;
4, 5, 6; 6, 5, 4; 5, 4, 6; 6, 5, 5;
4, 4, 5; 5, 5, 5; 4, 5, 6; 4, 5, 5;
4, 5, 4; 4, 6, 4; 5, 5, 6; 5, 5, 5;
3, 4, 3; 5, 6, 4; 3, 5, 5; 5, 6, 2;
4, 4, 4; 4, 5, 4; 5, 6, 5; 5, 5, 4;
5, 5, 5; 5, 5, 5: 5, 5, 6; 5, 6, 4;
3, 5, 4; 4, 5, 4; 5, 6, 5; 5, 5, 4;
4, 5, 5; 5, 6, 6; 5, 6, 5; 5, 5, 5;
5, 6, 5; 6, 5, 6; 5, 6, 5; 6, 6, 6;
3, 5, 6; 5, 6, 3; 6, 4, 5; 5, 5, 3;
4, 6, 5; 5, 6, 5; 6, 5, 5; 6, 5, 5;

5, 5, 4; 5, 5, 5; 6, 5, 5; 5, 5, 5;
5, 4, 5; 6, 5, 4; 5, 5, 6; 6, 4, 6;
5, 4, 4; 5, 5, 5; 6, 5, 4; 5, 5, 4;
5, 6, 5; 6, 5, 6; 6, 5, 6; 6, 6, 5;
3, 5, 5; 4, 6, 5; 5, 5, 5; 5, 5, 5;
3, 5, 4; 4, 5, 4; 5, 6, 5; 6, 4, 4;
4, 5, 5; 5, 5, 5; 5, 5, 5; 5, 6, 5;
3, 4, 5; 4, 5, 5; 6, 5, 5; 4, 5, 4;
3, 4, 5; 4, 6, 5; 5, 6, 4; 3, 5, 5;
4, 3, 5; 4, 5, 4; 4, 4, 6; 4, 4, 6;
3, 6, 4; 5, 6, 6; 4, 5, 5; 5, 5, 4;
5, 4, 6; 5, 5, 6; 5, 6, 5; 5, 5, 5;
3, 4, 4; 5, 6, 3; 3, 6, 3; 3, 6, 3;
4, 3, 5; 5, 5, 6; 5, 5, 5; 6, 4, 5;
4, 5, 4; 5, 5, 5; 4, 5, 5; 4, 6, 5;
5, 6, 4; 6, 5, 5; 5, 6, 4: 6, 5, 5;
*3, 3, 3; 3, 3, 4; 5, 3, 4; 3, 6;
5, 6, 5; 5, 6, 5; 5, 6, 5; 5, 6, 5;
6, 5, 6; 6, 5, 6; 6, 5, 6; 6, 5, 6;

Third Stage.

With not more than seven tentacles in any subdivision : —

7, 7, 7; 7, 7, 7; 7, 7, 7; 7, 7, 7; (2)
4, 7. 4; 5, 7, 5; 6, 6, 5; 6, 7, 6;
5, 7, 4; 7, 5, 5; 6, 7, 6; 6, 7, 6;
5, 7, 6: 5, 7. 6; 5, 7, 5; 5, 7, 6;
5, 6, 6; 5, 6. 7; 6, 7, 5; 6, 7, 6;
4, 5, 4; 5, 3, 5; 6, 5, 7; 4, 5, 6;
5, 5, 5; 5, 7, 5; 5, 6, 6; 5, 6, 6;
7, 7, 1; 6, 4, 6; 5, 7, 7; 6, 6, 7;
6, 5, 6; 6, 6, 7; 6, 7, 7; 7, 7, 7;
6, 5, 6; 5, 6, 7; 3, 7, 6; 6, 6, 6;
6, 7, 6; 6, 7, 7; 5, 7, 7; 5, 7, 6;
5, 6, 7; 4, 7, 3; 4, 7, 5; 7, 4, 3;
5, 7, 6; 7, 5, 5; 5, 6. 3; 5, 5, 5;
4, 4. 6; 5, 5, 5; 7, 6. 5; 4, 4, 5;
5, 6, 5; 7, 5, 5; 6, 6. 3; 5, 5, 5;
3, 5, 5; 5, 4, 3; 7, 6, 4; 4, 4, 3;
7, 7, 5; 5, 7. 5; 5, 5, 6; 5, 7, 4;
5, 6, 6; 7, 7, 5; 5, 6, 5; 6, 7, 7;
7, 7, 4; 5, 7. 5; 6, 7, 7; 5, 7, 5;
5, 6. 6; 6, 7. 7; 6, 7, 6; 7, 6, 4;
5, 6, 6; 7, 6, 6; 5, 6. 5; 6, 5, 6;
4, 6, 6; 6, 7. 5; 6, 5, 6; 5, 7, 4;
3, 5, 5; 6, 6, 7; 3, 4, 7; 6, 5, 5;

5, 6, 6; 6, 7, 5; 7, 5, 6; 5, 7, 5;
3, 3, 5; 5, 6, 6; 5, 7, 5; 5, 3, 5;
4, 4, 6; 4, 6, 5; 5, 5, 6; 7, 6, 2;
4, 7, 6; 5, 7, 5; 7, 7, 7; 7, 7, 5;
5, 5, 3; 5, 6, 7; 5, 4, 5; 5, 5, 7;
5, 2, 5; 6, 6, 5; 6, 7, 6; 6, 7, 4;
4, 7, 6; 5, 7, 5; 7, 7, 7; 7, 7, 5;
5, 5, 4; 5, 6, 6; 5, 5, 5; 4, 7, 5;
5, 6, 5; 5, 6, 5; 5, 7, 5; 6, 6, 6;
*5, 5, 4; 6, 7; 7; 5, 7, 6;
5, 6, 6; 6, 6, 5; 5, 7, 6; 5, 7, 7;
4, 3, 7; 5, 6, 6; 6, 5, 5; 6, 7, 4;
5, 6, 5; 6, 7, 6; 5, 7, 5; 6, 7, 4;
3, 7, 6; 6, 6, 2; 6, 6, 6; 5, 7, 6;
4, 4, 5; 4, 5, 5; 5, 4, 7; 5, 4, 4;
3, 6, 7; 5, 6. 5: 5, 7, 5; 6, 6, 5;
3, 7, 6; 5, 5. 2; 5, 6, 7; 5, 6, 6;
3, 5, 6; 6, 6, 5; 5, 6, 4; 4, 5, 7;
3, 2, 7; 6, 6, 5; 5, 6, 4; 4, 5, 7;
3, 5, 6; 6, 6. 5; 5, 6, 4; 5, 5, 7;
5, 6, 6; 6, 6, 6; 6, 7, 5; 6, 7, 6;
5, 7, 6; 6, 6, 6; 6, 6, 6; 6, 6, 6;
3, 7, 5; 4, 6, 4; 5, 6, 6; 5, 4, 6;

3, 6, 6; 4, 5, 5; 5, 6, 5; 5, 7, 3;
5, 7, 7; 6, 6, 7; 7, 6, 7; 7, 7, 7;
5, 5, 5; 6, 7, 6; 6, 6, 4; 5, 7, 5;
3, 7, 4; 5, 6, 4; 2, 5, 5; 5, 6, 3;
4, 7, 6; 6, 7, 5; 6, 7, 7; 7, 5, 7;
5, 6, 6; 5, 7, 5; 5, 6, 6; 6, 5, 6;
4, 4, 5; 4, 7, 4; 5, 5, 5; 4, 5, 5;
5, 6, 5; 6, 5, 7; 7, 5, 4; 6, 6, 6;
4, 5, 6; 6, 6, 5; 5, 6, 5; 5, 7, 6;
3, 4, 6; 6, 5, 6; 7, 4, 5; 5, 5, 5;
6, 6, 6; 6, 7, 6; 6, 7, 6; 6, 6, 6;
5, 5, 5; 5, 6, 5; 5, 7, 5; 5, 7, 5;
5, 3, 5; 5, 4, 5; 5, 6, 3; 3, 5, 7;
5, 6, 4; 6, 6, 6; 6, 5, 7; 5, 7, 6;
5, 5, 6; 6, 7, 6; 6, 7, 6; 6, 5, 4;
5, 7, 5; 7, 6, 6; 6, 7, 5; 6, 6, 6;
4, 7, 7; 7, 6, 6; 7, 6, 5; 6, 7, 6;
*5, 6, 6; 6, 6, 6; 6, 6, 6; 3, 3, 2, 3, 7;
4, 7, 7; 7, 7, 6; 6, 7, 7; 7, 7, 5;
5, 7, 6; 6, 6, 6; 7, 7, 6; 7, 7, 6;
5, 6, 6; 6, 7, 7; 7, 7, 6; 7, 7, 6;
5, 5, 7; 6, 5, 7; 7, 6, 6; 6, 7, 6;
5, 7, 5; 5, 7, 6; 6, 7, 6; 7, 7, 5;
*3, 6, 7; 5, 6, 4; 7, 6, 6; , 7, ;
4, 6, 4; 4, 6, 5; 5, 7, 4; 5, 7, 5;
5, 5, 7; 5, 6, 6; 6, 6, 5; 5, 7, 6;
5, 6, 6; 5, 6, 7; 6, 5, 7; 6, 4, 7;
5, 4, 6; 5, 4, 7; 6, 5, 7; 6, 7, 7;
5, 6, 4; 6, 5, 5; 5, 6, 4; 7, 5, 5;
5, 6, 6; 6, 6, 6; 7, 5, 6; 7, 7, 6;
3, 4, 3; 5, 7, 4; 4, 3, 4; 3, 4, 5;
*5, 7, 6; 5, 5, 4; 6, 7; 7;
*6, 5, 6; 7, 7, 5; 5, 3; 2, 3; 5, 5, 6;
*5, 6, 5; 6, 7, 5; 6, 3, 3; 5, 6, 5;
7, 7, 7; 7, 7, 7; 7, 7, 7; 7, 7, 7;
7, 7, 7; 7, 7, 7; 7, 7, 7; 7, 7, 7;
6, 7, 6; 6, 7, 6; 6, 7, 6; 6, 7, 6;

With not more than eight tentacles in any primary subdivision: —

6, 6, 7; 6, 7, 7; 7, 7, 7; 8, 7, 7;
5, 7, 6; 7, 6, 5; 6, 6, 5; 8, 7, 6;
6, 7, 5; 7, 7, 7; 8, 5, 4; 6, 7, 6;
3, 5, 4; 5, 5, 8; 5, 7, 8; 6, 7, 5;
4, 7, 6; 5, 7, 5; 8, 7, 7; 7, 7, 5;
*3, 5, 3; 6, 3, 4; 4, 5, 5; 8, 4;
7, 8, 7; 7, 8, 8; 8, 7, 8; 8, 7, 8;
*3, 3, 3; 3, 3, 4; 3, 5, 4; 8, 3;
5, 6, 7; 6, 7, 6; 8, 5, 5; 7, 5, 5;
5, 5, 5; 5, 7, 7; 6, 7, 5; 8, 5, 5;
4, 5, 5; 8, 4, 5; 5, 5, 5; 5, 5, 6;
*3, 3, 2; 4, 3, 1, 3; 4, 8, 2; 2, 3, 1;
3, 7, 5; 6, 7, 8; 5, 6, 6; 7, 7, 4;
5, 7, 7; 6, 8, 6; 6, 6, 6; 7, 7, 7;
5, 7, 7; 7, 7, 7; 6, 7, 7; 6, 7, 8;
5, 5, 6; 4, 7, 8; 7, 6, 5; 5, 6, 7;
5, 5, 7; 7, 6, 6; 6, 7, 6; 8, 5, 6;
5, 5, 5; 6, 6, 6; 5, 6, 6; 7, 8, 3;
5, 5, 5; 5, 6, 5; 5, 6, 5; 8, 7, 6;
5, 5, 6; 5, 8, 3; 4, 7, 6; 5, 7, 5;
6, 6, 7; 6, 6, 7; 8, 7, 6; 6, 7, 7;
*2, 3, 3; 3, 1, 3, 4; 1, 3, 2; 2, 8, 4;

With not more than nine tentacles in any subdivision: —

7, 3, 7; 9, 7, 7; 5, 7, 6; 6, 6, 5;
*6, 6, 7; 7, 7, 7; 9, 7; 7, 7, 7;
3, 9, 5; 7, 5, 5; 6, 5, 5; 5, 7, 7;
5, 3, 5; 5, 6, 5; 6, 3, 9; 5, 6, 6;
4, 7, 7; 5, 8, 7; 6, 9, 4; 7, 8, 7;
*3, 7, 5; 4, 7, 4; 4, 7, 4; 9, 4;
*4, 4, 3; 5, 6; 9, 4; 4, 4, 5;
6, 8, 6; 7, 7, 8; 8, 7, 7; 7, 9, 8;
*7, 4, 6; 7, 6, 1; 7, 9; 7, 5, 7; 7, 6, 6;
*3, 5, 3; 4, 5, 3; 1, 9, 5; 8, 3, 4;

With not more than ten tentacles: —

*2, 6, 6, 6, 9; 5, 6, 5; 7, 6, 10;
6, 8, 5; 7, 8, 8; 7, 4, 6; 10, 8, 9;
5, 10, 6; 7, 8, 6; 6, 6, 8; 6, 7, 8;
*5, 4, 5; 6, 5, 5; 6, 7, 5; 10, 5;
*3, 4, 4; 10, 1; 3, 5, 5; 4, 6, 6;
*5, 6, 7; 9, 5, 2; 3, 10; 8, 7, 6;

With not more than eleven tentacles : —

*11, 5; 11, 5; 5, 5, 5; 6, 5, 4;
2, 11, 5; 5, 9, 4; 5, 10, 3; 5, 7, 3;
8, 7, 9; 9, 7, 8; 11, 10, 10; 11, 7, 10;
*3; 11, 6; 5, 4, 2; 8, 8, 4; 7, 7, 8;
3, 11, 10; 6, 4, 8; 9, 8, 10; 6, 8, 4;
*4, 6, 5; 2, 8, 6, 7; 1, 11, 2;
*3, 5, 5; 4, 5, 6; 4, 11; 11, 2;
7, 8, 11; 10, 7, 7; 11, 6, 7; 11, 7, 6;

With not more than twelve tentacles : —

*5, 5, 5; 5, 6, 6; 7, 6, 6; 12, 7;
*6, 7, 6; 6, 7, 7; 7, 7, 7; 12, 5;
*5, 7, 4; 4, 7, 6; 5, 7, 4; 12, 5;
*3, 6, 2; 3, 3; 10, 9, 9; 10, 7, 8;
8, 7, 12; (2 forks).

With not more than thirteen tentacles : —

*5, 6, 4; 6, 13; 6, 7, 4; 5, 7, 7;
*8, 3, 13; 5; 11, 8, 11; 12, 7, 10;
*4, 4, 5; 6, 4, 4; 13, 5; 5, 6, 4;
*9, 7, 8; 10, 7, 10; 13, 9, 7;

With not more than fourteen tentacles : —

*7, 7, 7; 8, 7, 8; 5, 7, 6; 14, 7;
*7, 6, 5; 7, 8; 1, , 10; 14;
*5, 7, 7; 6, 7, 6; 7, 8, 7; 9, 14;

Fourth Stage.

With not more than fifteen tentacles : —

*2, 5, 5; 2, 15, 6, 7; 9, 10; 9, 2;
*6, 6, 7; 6, 15; 6, 2; 1, 8, 6;
*5, 6, 5; 15, 6; 6, 7, 7; 7, 6, 7;
*6, 7, 10; 6, 7, 15; 12, 14, 5;
*7, 8, 6; 6, 15; 3, 15; 7, 8, 7;

With not more than seventeen tentacles : —

*17; 15; 15; 16; no otoliths.

With not more than eighteen tentacles : —

*6, 6, 6; 7, 7; 9; 18, 7;
*9, 7, 9; 18, 7; 11, 17; 11, 18;

With not more than twenty tentacles : —

*7, 6, 7; 7, 7, 8; 8; 1, 8; 20, 8;

With not more than twenty-seven tentacles : —

*9, 6, 8; 27; 8, 11;

Table showing Variations in the number of Radial Canals, of Quadrants, of Primary Divisions of Quadrants, or of the Otoliths.

Irregular.	Number of Otoliths.	Number of Radial Canals.
6, 7; 7; 5, 7, 6; 5, 5, 4;	5	4
11, 5; 11, 5; 5, 5, 5; 6, 5, 4;	6	4
5, 7, 6; 14, 7; 7, 7, 7; 8, 7, 8;	7	4
5, 5, 5; 5, 6, 6; 7, 6, 6; 12, 7;	7	4
3, 5, 3; 6, 3, 4; 4, 5, 5; 8, 4;	7	4
6, 7, 6; 6, 7, 7; 7, 7, 7; 12, 5;	7	4
1, 3, 3; 3, 3, 3; 3, 3, 3; 3, 3;	7	4
6, 6, 7; 7, 7, 7; 9, 7; 7, 7, 7;	7	4
5, 7, 4; 4, 7, 6; 5, 7, 4; 12, 5;	7	4
5, 6, 4; 6, 13; 6, 7, 4; 5, 7, 7;	7	4
6, 6, 6; 7, 7; 9; 18, 7;	4	4
8, 3, 13; 5; 11, 8, 11; 12, 7, 10;	6	4
2, 5, 5; 2, 15, 6, 7; 9, 10; 9, 2;	7	4
3, 6, 2; 3, 3; 10, 9, 9; 10, 7, 8; 8, 7, 12;	9	5
2, 6, 6; 6, 9; 5, 6, 5; 7, 6, 10;	7	4
3, 3, 3; 3, 3, 4; 3, 5, 4; 8, 3;	7	4
7, 6, 5; 7, 8; 1, , 10; 14;	5	4
3, 3, 3; , 3, 3, 2; 4, 3, 2, 2; , 5, 3;	9	4
3; 11, 6; 5, 4, 2; 8, 8, 4; 7, 7, 8;	7	5
3, 3, 2; 4, 3, 1, 3; 4, 8, 2; 2, 3, 1;	9	4
5, 6, 6; 6, 6, 6; 6, 6, 6; 3, 3, 2, 3, 7;	10	4
6, 6, 7; 6, 15; 6, 2; 1, 8, 6;	6	4
3, 7, 5; 4, 7, 4; 4, 7, 4; 9, 4:	7	4
3, 6, 7; 5, 6, 4; 7, 6, 6; , 7 ,;	8	4
17; 15; 15; 16;	0	4
5, 4, 5; 6, 5, 5; 6, 7, 5; 10, 5;	7	4
4, 6, 5; 2, 8, 6, 7; 1, 11, 2;	7	3
4, 4, 5; 6, 4, 4; 13, 5; 5, 6, 4;	7	4
4, 4, 3; 5, 6; 9, 4; 4, 4, 5;	6	4
3, 4, 4; 10, 1; 3, 5, 5; 4, 6, 6;	7	4
3, 5, 5; 4, 5, 6; 4, 11; 11, 2;	6	4
9, 7, 9; 18, 7; 11, 17; 11, 18;	5	4
5, 6, 5; 15, 6; 6, 7, 7; 7, 6, 7;	7	4
5, 6, 7; 9, 5, 2; 3, 10; 8, 7, 6;	7	4
7, 4, 6; 7, 6, 1; 7, 9; 7, 5, 7; 7, 6, 6;	9	5
6, 7, 10; 6, 7, 15; 12, 14, 5;	6	3
9, 7, 8; 10, 7, 10; 13, 9, 7;	6	3
5, 7, 7; 6, 7, 6; 7, 8, 7; 5, 7, 7; 9, 14;	9	4
3, 3, 3, 3, 3, 4; 5, 3, 4; 3, 6;	7	4
7, 8, 6; 7, 8, 7: 6, 5; 3, 15;	6	4
5, 7, 6; 5, 5, 4; 6, 7; 7, ;	6	4

Irregular.	Number of Otoliths.	Number of Radial Canals.
7, 6, 7; 7, 7, 8; 8; 1, 8; 20, 8; . .	6	5, 1 forking.
9, 6, 8; 27; 8, 11;	3	3
6, 5, 6; 7, 7, 5; 5, 3; 2, 3; 5, 5, 6; .	8	5
7, 6, 5; 7, 8; 1, , 10; 14;	5	4
2, 3, 3; 3, 1, 3, 4; 1, 3, 2; 2, 8, 4; .	9	4
6, 6, 7; 6, 15; 6, 2; 1, 8, 6;	6	4

On Plate IX. will be found a number of diagrammatic figures giving an idea of the irregular growth of the marginal tentacles. The lengths of the tentacles are drawn as fully expanded, the position of the radial and circular canals is indicated, and the otolith tentacles are marked by a cross. The structure and length of the marginal tentacles of Eucope are such that the comparative length of adjoining tentacles is readily observed, owing to the slight degree of contraction and expansion they possess.

In Figures 1 to 6, 10, and 14 (Plate IX.), we have the normal number of tentacles (seven) in each of the primary quadrantic subdivisions. It is noticeable that t_1 can only in the case of Figures 4 and 10 be distinguished from the two t_2, while the four t_3 are of nearly uniform size in all the figures except Figure 6.

In Figures 7, 12, 13, 16, 17 (one primary division), 18, 19, and 22–26, there are only five marginal tentacles in each primary quadrantic division. In the greater number of these figures it is possible to distinguish t_1, or t_1 and t_2, while the irregularly developed tentacles are part of the t_3 cycle. In Figures 20–22 (one sector), and 27–29 (two sectors), the cycles t_1 and t_2 can be distinguished, and the irregularity of development occurs in the t_3 cycle, which may appear at different points of the circular canal, as is seen by comparing Figures 20–22, 27, and 28.

Figures 8–10, 17, 22, 29, and 30 show the irregularity in time of the development of the marginal tentacles in the different sectors of the same quadrant, as well as the irregularity in the growth of the three cycles t_1–t_3 in adjoining sectors. In Figures 8, 29, and 30, the marginal tentacles between the otoliths are in the same stage of growth, but the tentacles of the right or left sectors are in very different stages of growth. In one case (Fig. 30) only one t_1 is developed in each sector; in Figure 29 the cycles of t_1 and t_2 are normal, while they are most irregular in the sectors of Figure 8.

When six marginal tentacles occur in one sector the irregularities in the t_2 and t_3 cycles are very marked (see Figs. 8, 9, 11, 15, and 17); t_1 can only be distinguished from the t_2 pair by its position.

The coalescence at the base of adjoining marginal tentacles to form a double tentacle with two spurs and two lashes is not uncommon. During the summer there were fourteen specimens met with having double tentacles; in all except two cases they were connected with the tentacle riding a sense organ.

The sensory tentacles usually have only one otolith; we however observed thirteen cases in which each sense organ contained two (Plate VIII. Figs. 15, 17), and five in which there were three otoliths (Plate VIII. Figs. 14, 16), and one in which there were no otoliths in any of the quadrants.

An examination of the table on page 137, in which the more interesting of the variations observed have been collected, will show how large a number of specimens show great variation in the number of the sense-bearing tentacles. Among specimens of Eucope with the normal number of quadrants we find the otoliths bearing tentacles vary from eight, the normal number, two in each quadrant, to three on one side and ten on the other. As will be noted, there are only five cases in which the sensory tentacles are greater in number than in the norm, while the number of cases in which they are suppressed is quite large. Their increase does not always accompany an increase in the number of radial canals. Two out of four specimens with five radial canals possessed nine sensory tentacles, another only seven, and one eight.

There seems to be no correlation between the number of marginal tentacles in any sector and the number of sensory tentacles.

The primary sector with the largest number of tentacles has often only one sensory tentacle, while that with a smaller number has two.

In a specimen with quadrants of unequal size, and with an unequal number of marginal tentacles, in each of which the formula is

7; 6; 4, 5, 5; 6, 7, 5;

there are six otoliths, one on each of the tentacles at the base of the radial canals between the first and second and the second and third quadrants, and the others as marked by the comma in the third and fourth quadrants.

In another specimen with very unequal quadrants there are nine otoliths, there being three in the largest quadrant, as shown by its formula. the first quadrant being the smallest, the last the largest:

1, 3, 2; 2, 8, 4; 2, 3, 3; 3, 1, 3, 4;

In a specimen in which two small quadrants are adjacent, there are only six otoliths. Taking the two smaller quadrants first, the formula is

6, 2; 1, 8, 6; 6, 6, 7; 6, 15;

The last quadrant is the largest.

The formula of another specimen, with unequal quadrants, is,

6, 6, 6; 7, 7; 9; 18, 7;

This shows only four otoliths, one quadrant without any, and two with only one.

In a similar specimen with a formula of

11, 8, 11; 12, 7, 10; 8, 3, 13; 5;

there are only six otoliths, with three normal quadrants, one not having any sense organs.

In a specimen with two adjoining radial canals forking below the genitals, making four quadrants with two small sectors cut out of two of them, there are ten otoliths, the formula being

$$10,\ 9,\ 9;\ 10,\ 7,\ 8;\ 2,\ 6,\ \overbrace{2,\ 8,}\ 7,\ 12;\ 3,\ \overbrace{3;\ 10,\ 1};$$

In a second specimen, forking similarly at the extremity of one radial canal, the formula was

$$7,\ 6,\ 7;\ 7,\ 7,\ 8;\ 8;\ \overbrace{1,\ 8;\ 20,\ 8};$$

In a specimen with an eccentric digestive cavity and quadrants unequally developed, the formula is

14; 7, 6, 5; 7, 8; 1, , 10;

or only five otoliths, neither the first nor the third quadrant having otoliths, while the fourth has two side by side.

In a specimen with equally developed quadrants, but with a long spur above the genitals at right angles to the radial canal, barely reaching the marginal canal, the formula is

$$\overbrace{3;\ 11,\ 6};\ 5,\ 4,\ 2;\ 8,\ 8,\ 4;\ 7,\ 7,\ 8;$$

there being three tentacles between the fork (spur) and the nearest canal.

In a very irregularly developed specimen, with the formula

6, 6, 6; 7, 7; 9; 18, 7;

there were only three otoliths.

In a specimen with only three radial canals, one of which forks above the genitals, the formula is

$$2, 15, 6, 7;\ 3, 10, 1;\ 9, \overbrace{2;\ 2}, 5, 5;$$

the otoliths being normal in number, but irregular in their distribution.

In another Eucope with three radial canals, we find seven otoliths represented in the formula

1, 11, 2; 4, 6, 5; 2, 8, 6, 7;

the last sector being somewhat larger than the others.

In a specimen with three equally developed sectors with the formula of

12, 14, 6; 6, 7, 10; 6, 7, 15;

there are six otoliths, the normal number in each sector, but the other marginal tentacles are most irregularly developed.

In still another Eucope, similar to the preceding one, with three sectors of equal size and well developed genitals with six otoliths, two in each sector, the formula was

10, 7, 10; 10, 9, 7; 9, 7, 8;

Finally, a Eucope with three quadrants of the same size had only three otoliths; its formula is

9, 6, 9; 27; 8, 9;

The formation of spurs (Plate VIII. Figs. 4–13) takes place usually at the base of the marginal tentacle, at its connection with the circular canal, but cases have been observed in which the spur shoots off from the lash of the tentacle (Plate VIII. Fig. 5). The formation of spurs is often accompanied by the atrophy of the inframarginal knob of the marginal tentacles (compare Plate VIII. Figs. 9–13, with Figs. 4–8).

It will be noticed that in the numerical variation of the segments the tendency is not to doubling the number of normal (4) segments, but either to add one or two, or to reduce the segments to three.

In Sarsia, Agassiz observed a specimen with six radial canals and Romanes one with five; he also observed a Sarsia with six radial canals, six ocelli, and six tentacles, like that seen by Agassiz, the only specimen in thousands examined.

According to Bateson, the numerical variations in Aurelia tend in two directions, i. e. to forms with six and twelve segments instead of the normal eight.

The same tendency in Aurelia to vary in the direction of six and twelve segments was pointed out by Brown, and was also noted in the older papers of Ehrenberg and Romanes.

According to Romanes, monstrous forms of Aurelia aurita are of frequent occurrence. Abnormality consisted in multiplicity and abortion of parts. All cases of asymmetrical multiplication applied to lithocysts, and always occurred in the same manner. When there were nine instead of eight lithocysts, the extra one was always fully developed and in close proximity to one of the normal lithocysts.

In symmetrical abnormalities all parts of the organism were equally affected. Thus all examples of multiplication extended proportionally to ovaries, nutritive canals, lithocysts, and tentacles, the effect being to increase the number while adhering to the type of the natural segments. In all cases the degree of abnormality was the same; e. g. 6 ovaries, 24 unbranched radial tubes, 12 lithocysts, and a six-lobed manubrium. All parts and segments thus increased one third their normal number. Romanes calls attention to the fact that this is the same proportional increase as in Sarsia, with six canals, and explains it as accidental. Supernumerary lithocysts always occur at the ends of the faintly colored radial tubes, never at the ends of the darker ones.

Segments and lobes of the manubrium may be multiplied without the ovaries increasing in number. Again, segments may multiply and manubrium and ovaries remain normal. Processes of multiplication may not extend to all quadrants of the umbrella. Multiplication of parts may be confined to one side of the umbrella, thus doubling or tripling organs on one side only.

Abnormalities usually are symmetrical. When they are not, the manubrium and ovaries are not affected, the segments only being multiplied. Abortion of parts takes place in the same symmetrical way as multiplication: there may be one ovary and six segments, and three ovaries instead of eight and four. Segments and ovaries may also be reduced to one half the normal number. In these two cases the manubrium is not affected. Abortion of parts was observed in the ovaries only. Partial suppression of ovaries was of frequent occurrence. The most prevalent case was where one ovary was smaller than the other three. Reduction also occurs in two alternating ovaries (i. e. opposite?). Sometimes three adjacent ovaries were reduced in size.

Total suppression of one ovary was more rare. Only in twelve cases in thousands was total suppression of two ovaries observed: sometimes it was two adjacent ones, and more frequently the two opposite ones that were absent. In one case three ovaries were absent, the specimen being otherwise fully developed. In no case was it observed that deficiency or absence of ovaries entailed a corresponding deficiency or absence of other organs. Reduction or suppression does not occur in any other organ than ovaries in A. aurita.

H. C. Sorby found, among A. aurita collected in Suffolk and Essex, a "few per thousand" abnormal specimens exhibiting sixfold, fivefold, threefold, and partial twofold symmetry. References to variations in Aurelia, Clavatella, Sarsia, and Stomobrachium may be found also in Bateson's "Materials for the Study of Variation," pp. 421–429. Edward T. Browne examined 383 specimens of A. aurita. He found that eight specimens (2.08%) exhibited numerical variations in the genital sacs, buccal arms, and tentaculocysts. The number of the genital sacs and of the buccal arms varied from three to six. He concludes that there appeared to be a correlation between genital sacs and buccal arms, but that the tentaculocysts vary independently of these. Eighty-seven cases (22.8%) showed variation in the number of tentaculocysts. Twenty of these had less, and the remainder more, than the normal number. The range of variation in tentaculocysts was 6 to 15.

The preceding observations on the variations of Aurelia show some striking differences from those we have made on Eucope. While in Aurelia there is a general correlation between the number of segments of genital sacs, of buccal lobes, and of tentaculocysts, there is no such correlation in the variations of Eucope. The sense organs in Eucope vary, both in number and in position, irrespectively of the number of radial canals and of segments. Neither multiplication nor abortion of parts in Eucope is symmetrical. The suppression of genital sacs is quite common in Eucope, while it is rare in Aurelia. In Eucope suppression is not limited to genital sacs; as in Aurelia, it extends to the otolith-bearing tentacles. As far as we have observed, the number of terminal folds of the manubrium does not vary in Eucope, and is not correlated to the number of segments.

The apparatus used in making the photographs was the large photomicrographic apparatus of Zeiss, with some modifications, direct sunlight being employed by means of a heliostat of the automatic kind, and all exposures were instantaneous. The camera was always used in the horizontal position, so that with an objective of low power the full length of the bellows could be employed to obtain sufficient magnification with the least loss of light. The objectives employed in photographing Eucope were those of 35 and 70 mm. focus, the lower power being employed with the larger specimens. The exposures were made twelve segments was pointed out by Brown, and was also noted in the older papers of Ehrenberg and Romanes.

According to Romanes, monstrous forms of Aurelia aurita are of frequent occurrence. Abnormality consisted in multiplicity and abortion of parts. All cases of asymmetrical multiplication applied to lithocysts, and always occurred in the same manner. When there were nine instead of eight lithocysts, the extra one was always fully developed and in close proximity to one of the normal lithocysts.

In symmetrical abnormalities all parts of the organism were equally affected. Thus all examples of multiplication extended proportionally to ovaries, nutritive canals, lithocysts, and tentacles, the effect being to increase the number while adhering to the type of the natural segments. In all cases the degree of abnormality was the same; e. g. 6 ovaries, 24 unbranched radial tubes, 12 lithocysts, and a six-lobed manubrium. All parts and segments thus increased one third their normal number. Romanes calls attention to the fact that this is the same proportional increase as in Sarsia, with six canals, and explains it as accidental. Supernumerary lithocysts always occur at the ends of the faintly colored radial tubes, never at the ends of the darker ones.

Segments and lobes of the manubrium may be multiplied without the ovaries increasing in number. Again, segments may multiply and manubrium and ovaries remain normal. Processes of multiplication may not extend to all quadrants of the umbrella. Multiplication of parts may be confined to one side of the umbrella, thus doubling or tripling organs on one side only.

Abnormalities usually are symmetrical. When they are not, the manubrium and ovaries are not affected, the segments only being multiplied. Abortion of parts takes place in the same symmetrical way as multiplication: there may be one ovary and six segments, and three ovaries instead of eight and four. Segments and ovaries may also be reduced to one half the normal number. In these two cases the manubrium is not affected. Abortion of parts was observed in the ovaries only. Partial suppression of ovaries was of frequent occurrence. The most prevalent case was where one ovary was smaller than the other three. Reduction also occurs in two alternating ovaries (i. e. opposite?). Sometimes three adjacent ovaries were reduced in size.

Total suppression of one ovary was more rare. Only in twelve cases in thousands was total suppression of two ovaries observed: sometimes it was two adjacent ones, and more frequently the two opposite ones that were absent. In one case three ovaries were absent, the specimen being otherwise fully developed. In no case was it observed that deficiency or absence of ovaries entailed a corresponding deficiency or absence of other organs. Reduction or suppression does not occur in any other organ than ovaries in A. aurita.

H. C. Sorby found, among A. aurita collected in Suffolk and Essex, a "few per thousand" abnormal specimens exhibiting sixfold, fivefold, threefold, and partial twofold symmetry. References to variations in Aurelia, Clavatella, Sarsia, and Stomobrachium may be found also in Bateson's "Materials for the Study of Variation," pp. 421–429. Edward T. Browne examined 383 specimens of A. aurita. He found that eight specimens (2.08%) exhibited numerical variations in the genital sacs, buccal arms, and tentaculocysts. The number of the genital sacs and of the buccal arms varied from three to six. He concludes that there appeared to be a correlation between genital sacs and buccal arms, but that the tentaculocysts vary independently of these. Eighty-seven cases (22.8%) showed variation in the number of tentaculocysts. Twenty of these had less, and the remainder more, than the normal number. The range of variation in tentaculocysts was 6 to 15.

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The most difficult task was to confine the animals to be photographed, more particularly with the microscope in the horizontal position. The device which proved most serviceable for flat or discoidal objects was a parallel compressor of the model of Hermann Fol. Rings were cut from pure rubber tissue of different thicknesses, the ring to be employed for any particular object being a little thicker than the object itself. The rubber ring was then placed on the lower plate of the compressor and pressed into contact with it by means of the finger. The object is then brought into the centre of the ring, and water added with a pipette until the inside of the ring is completely filled, and the upper part of the compresser carefully screwed down until it comes in contact with the rubber, the superfluous water being at the same time squeezed out. If this be done with care, the inside of the ring will be completely filled with water and contain no air bubbles. There should be just enough pressure to allow the upper glass of the compressor to come in contact with the object. This can be determined by holding the compressor vertically, and screwing down the upper plate until the object ceases to sink. The compressor can now be clamped to the stage of the microscope in any position. By employing rubber rings of sufficient thickness, aquaria can be contrived in this way one eighth of an inch in depth. In photographing the rounder and plumper forms, any pressure upon the animal would produce a sensible change in shape. Such forms, therefore, were placed in small deep watch glasses and confined by glass rings, the microscope being placed in a vertical position, the camera however remaining horizontal. The connection between the microscope and camera was effected by means of the prism end of an Oberhäuser's camera lucida, to which the light tight collar had been adjusted by means of an adapter. The light in this case was centred upon the substage mirror of the microscope, and thus upward. Jellyfish that have been for some time in a small quantity of sea water become partially stupefied by the consumption of the air in the water, and are then more quiet and their tentacles are better extended.

For larger objects, such as Medusæ and Ctenophora, a Zeiss series II.^{a} 1 : 8 photographic lens with an iris shutter was made use of. A reversing prism fastened to the front of the lens allows the use of a horizontal camera in photographing animals in open dishes. Work of this description is done out of doors, illumination being obtained by a series of mirrors, the arrangement of which varies with the nature of the object and the view desired. The work is still in an experimental stage, and it is hoped to give in a subsequent paper a more detailed account of methods and results.

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EXPLANATION OF PLATES.

Plates I.–VI., from photographs taken by W. McM. Woodworth.

PLATE I.

To illustrate the variation in the development of the genital organs. The diameter of the disk of the specimens of Eucope figured varied from 3.5 to 4.5 mm.

Fig. 1. Adult male, with equally developed genitals, their formula being 1, 1, 1, 1,
Fig. 2. Adult male, with only three fully developed genitals, their formula being 1, 1, 1, 4,
Fig. 3. Male, with the genital formula 1, 2, 3, 4, all in different stages of development.
Fig. 4. Female with two atrophied genitals, formula being 1, 1, 0, 0,
Fig. 5. Male of the formula 1, 1, 3, 4,
Fig. 6. Male with only one large genital pouch, with the formula 1, 4, 4, 4,

PLATE II.

Fig. 1. Male, with two atrophied genital organs, and with unequally developed radial canals, three of which have spurs running at a slight angle from them.
Fig. 2. Male, with unequally developed genitals, and with one radial canal forking both above and below the genital pouch.
Fig. 3. Young Eucope with undeveloped genital organs.
Fig. 4. Male Eucope with spurs on two of the radial canals, with unequally developed genitals.
Fig. 5. Female with only two fully developed genital pouches, and one atrophied radial canal.
Fig. 6. Male with genital formula 1, 1, 1, 0,

PLATE III.

Figures of Eucope having three or more radial canals, and forking either above or below the genital organs.

Fig. 1. Eucope with three radial canals, one of which forks at the extremities of the heart-shaped genital pouch.

Fig. 2. Male Eucope with four radial canals, also forking at the genital pouch. Nearly equally developed genitals.

Fig. 3. Female Eucope with three radial canals, one of which sends off a prominent spur above the rudimentary genital pouch. Genitals very unequally developed.

Fig. 4. Male with three radial canals, one of which forks well above the genital organs of the branches. Genital organs nearly equally developed.

Fig. 5. Male with four radial canals. The genital organs corresponding to the forks of one of the canals are barely united. Genital pouch atrophied in one quadrant.

Fig. 6. Male Eucope with three unequally developed genital organs.

PLATE IV.

With figures of Eucope having five or more radial canals.

Fig. 1. Female Eucope with five radial canals and the same number of unequally developed genital pouches, with the formula 1, 2, 3, 4, 5,

Fig. 2. Young male Eucope with five radial canals, unequally developed genitals, and a sixth rudimentary radial canal.

Fig. 3. Female Eucope with five radial canals, two fully developed genital pouches, one less so, and two radial canals without genital organs.

Fig. 4. Female Eucope with five radial canals, and only one fully developed genital pouch.

Fig. 5. Female Eucope with five radial canals, one of which is atrophied below the genital pouch. Genital organs unequally developed.

Fig. 6. Female Eucope with five radial canals and unequally developed genitals, one of the canals having no genitals, and forking.

PLATE V.

Fig. 1. Male Eucope with five radial canals and five nearly equally developed genital pouches.

Fig. 2. Male Eucope with five radial canals and traces of a sixth, and very unequally developed genitals.

Fig. 3. Female Eucope with five radial canals subdividing the disk into very unequal segments, only two of the genital organs fully developed.

Fig. 4. Female Eucope with unequally developed genitals, but with five very symmetrical segments.

Fig. 5. Female with five radial canals, one of which forks at the periphery, and five very unequally developed genitals.

Fig. 6. Male with five radial canals, unequally developed genitals, and segments of unequal size.

PLATE VI.

Fig. 1. Male Eucope with five radial canals, one of which forks above the genitals close to the base of the digestive cavity, dividing the disk into six different-sized sectors.

Fig. 2. A male Eucope similar to Figure 1, with more fully developed genitals.

Fig. 3. Young Mnemiopsis Leidyi A. Ag., magnified $\frac{1}{3}$.

Fig. 4. Doliolum sp. in profile, magnified $\frac{30}{1}$.

Fig. 5. Annellid larva (Aricidea?), magnified $\frac{100}{1}$.

Fig. 6. Ectopleura ochracea A. Ag., seen in profile, magnified $\frac{30}{1}$.

PLATE VII.

To illustrate the formation of spurs, branches, and anastomosing canals from the sides of the radial canals.

Fig. 1. Slightly projecting spurs on side of radial canal.

Figs. 2, 3, 6, 7, and 10 show quite prominent hook-like lateral prolongations from the sides of the radial canals.

Figs. 4, 5, and 9 show forks of the radial canals in Figure 4 above the genitals, in Figure 5 below.

Fig. 4 shows a transverse canal connecting adjoining radial canals.

Fig. 8 shows a circular canal connecting the radial canals below the base of the manubrium.

PLATE VIII.

Fig. 1. Marginal sense-bearing tentacle with three otoliths.

Figs. 2 and 3 show the coalescence of adjoining marginal tentacles, Figure 2 with one otolith, Figure 3 with two.

Figs. 4–13 show the mode of formation of an abnormal basal spur frequently seen jutting out from the marginal tentacles, either with or without otoliths.

Figs. 14–17 show the numerical variation of the otoliths in the sense organ of the marginal tentacle.

Fig. 18 shows the coalescence of male genital organs of adjoining radial canals.

Fig. 19 shows the formation of a radial canal shooting up from the circular canal.

Fig. 20. An abnormal Eucope with confluent radial canals and ovaries developed on the main and the lateral canal.

Fig. 21 shows lateral leaf-like expansions of male genital organs which have not as yet run together, as in Figure 18.

PLATE IX.

To illustrate the irregular development of the marginal tentacles belonging to the t_1, t_2, and t_3 cycles.

Figs. 1–6, 10, and 14 are normal sectors belonging to the third stage of development.

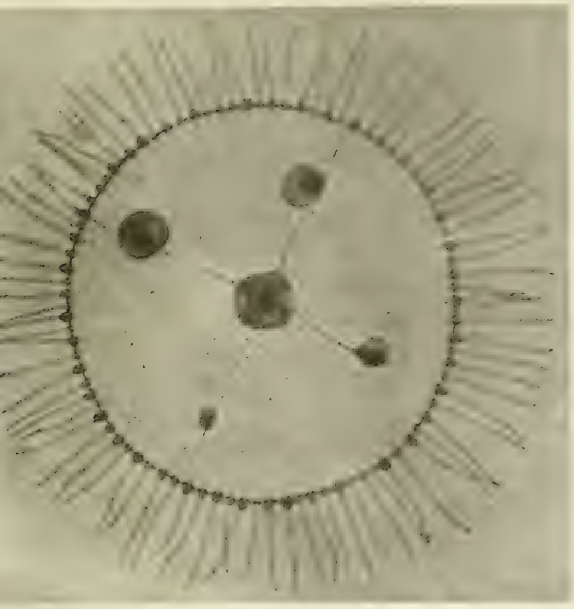
Figs. 7–9, 12, 13, 16–19, and 22–26 show sectors belonging to the same stage of development, but there has been great irregularity in the succession and growth of the third cycle of tentacles.

Figs. 20–22, 27, and 28 show sectors with only one tentacle of the t_3 cycle in each primary division.

Figs. 29 and 30 belong to the second stage of development.

PLATE I.

3



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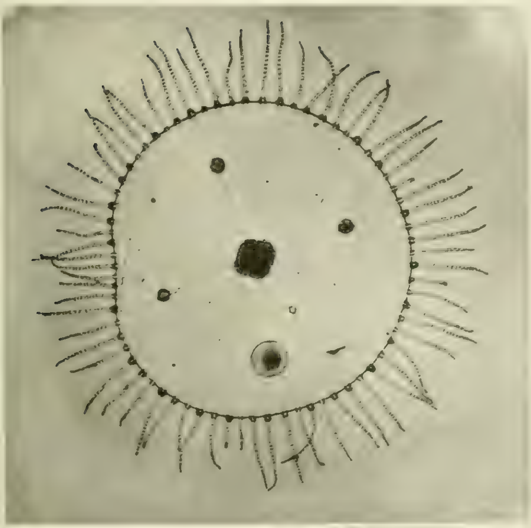

ARTOTYPE, E. BIERSTADT, N. Y.

EUCOPE

PLATE I

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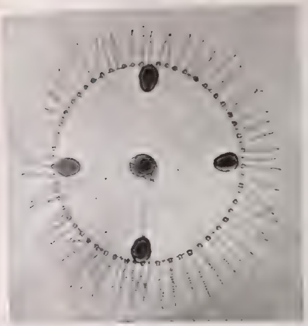

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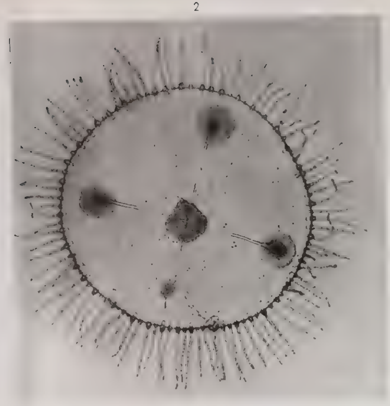

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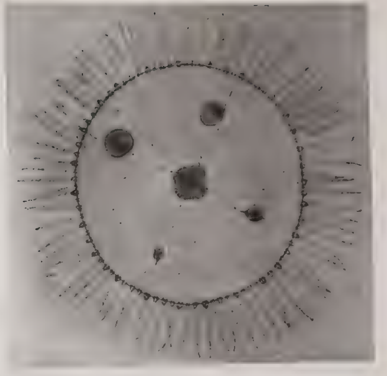

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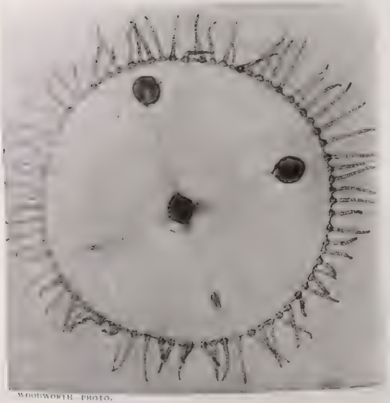

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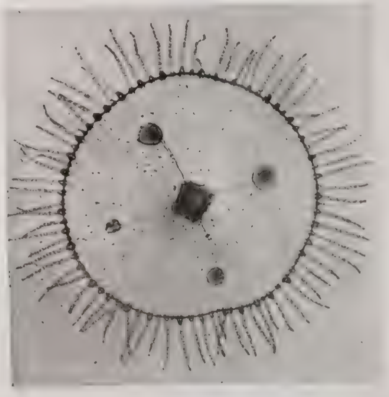

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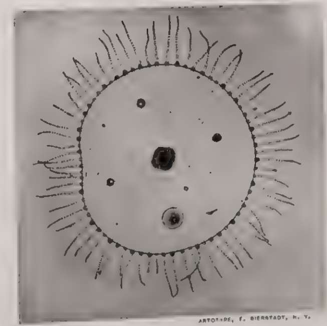

WOODWORTH PHOTO.

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PLATE III.

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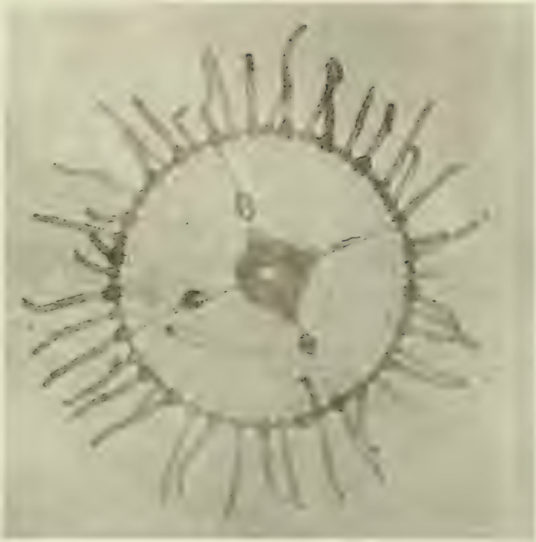

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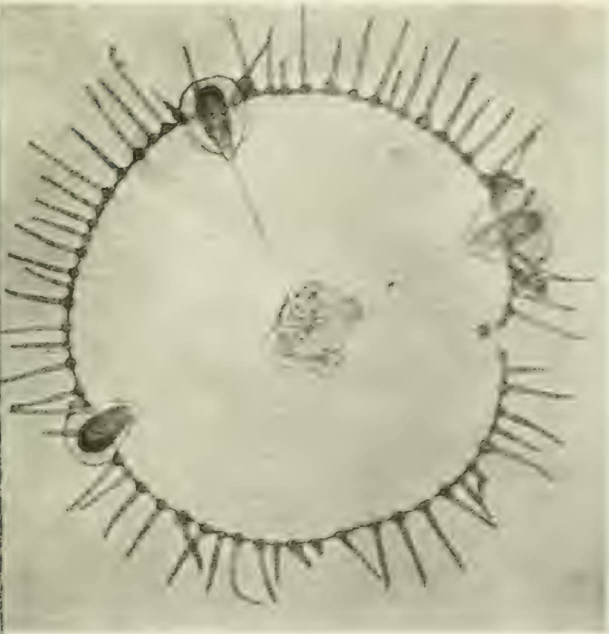
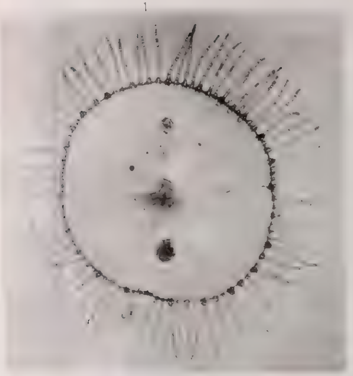


ARTOTYPE, E. BIERSTADT, N. Y.

EUCOPE

PLATE II.

1



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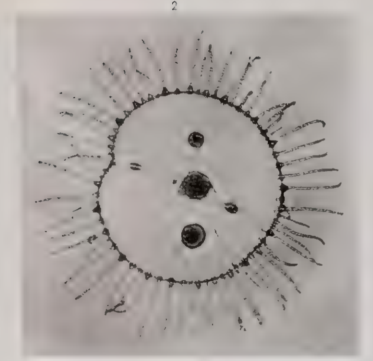

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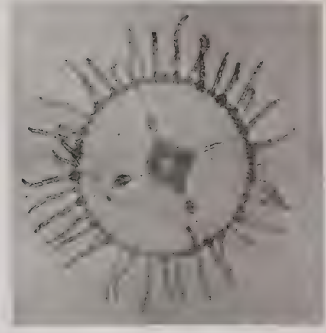

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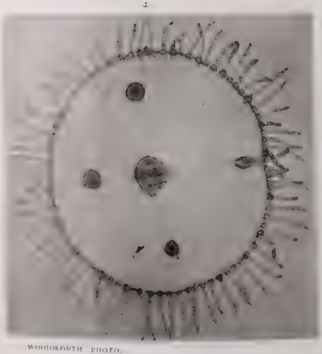

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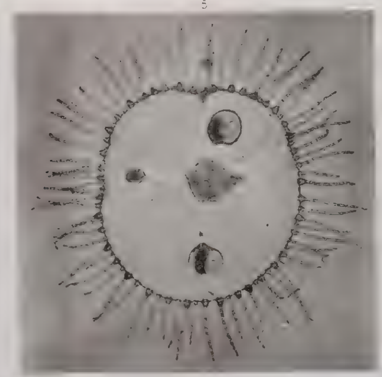

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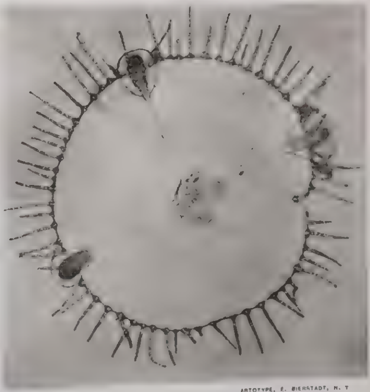

WOODWORTH PHOTO.

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PLATE III.

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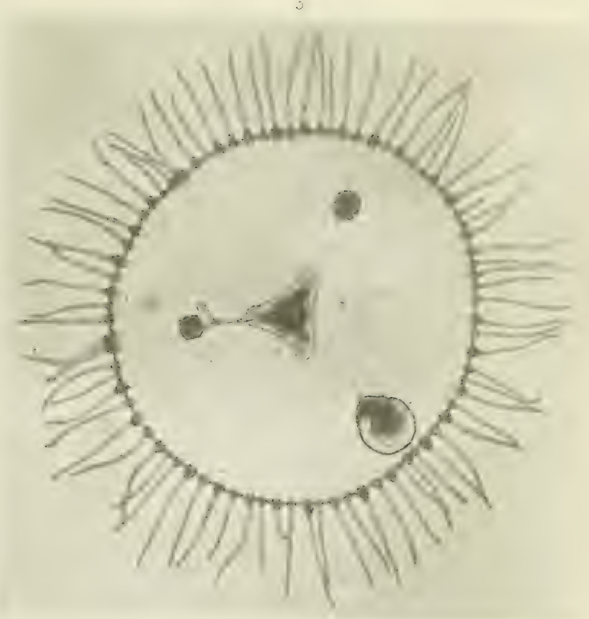

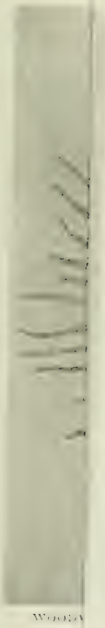

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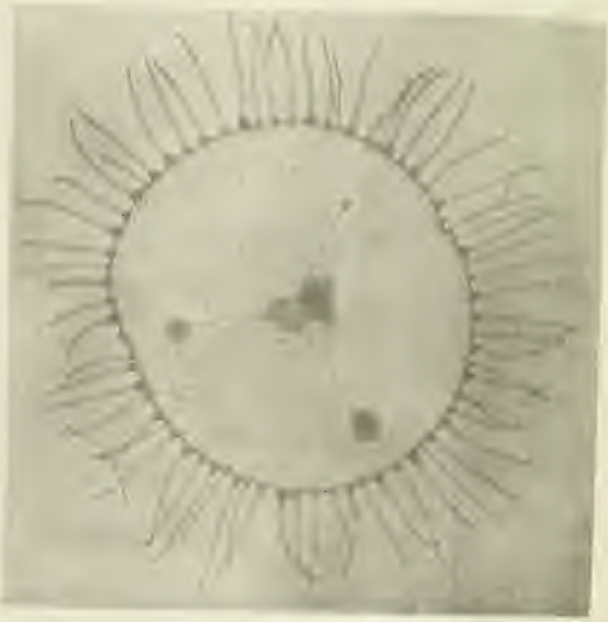


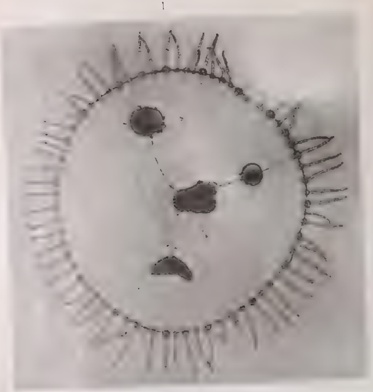
Wood

ARTOTYPE, E. BIERSTADT, N. Y.

EUCOPE

PLATE II

1



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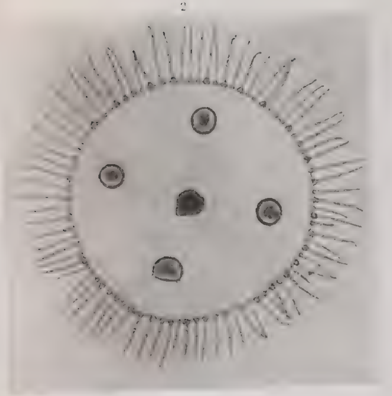

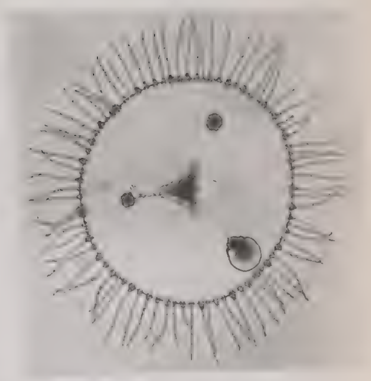

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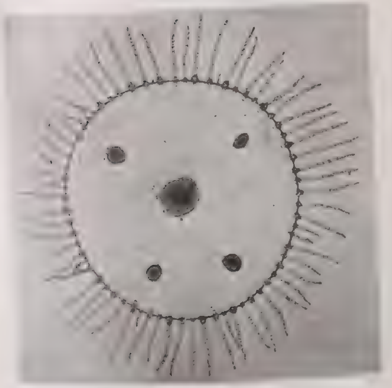

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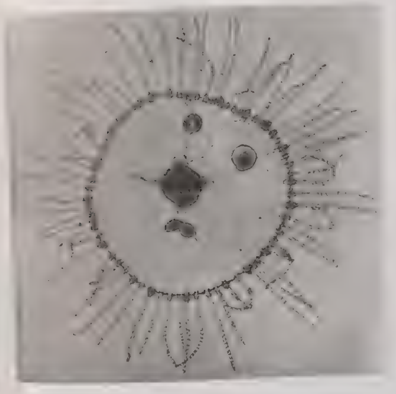

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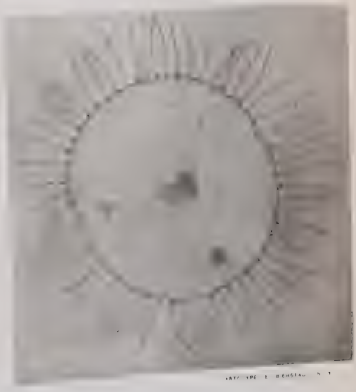


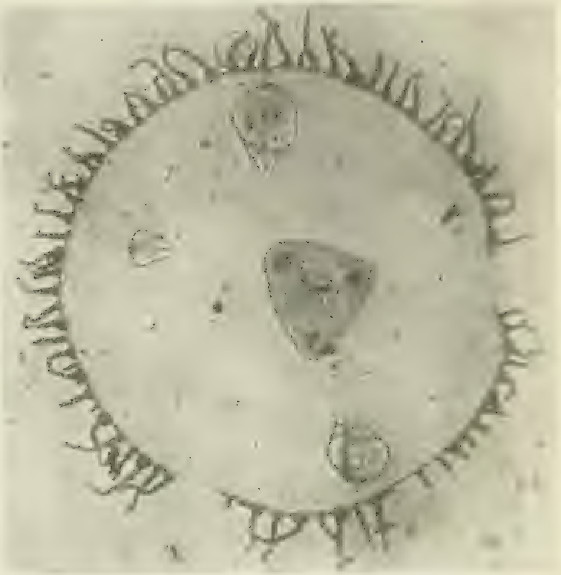
WOODWORTH, PHOTO.

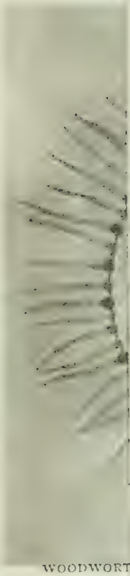
ARTOTYPE E. BIERSTADT, N.Y.

EUCOPE

PLATE IV.

3





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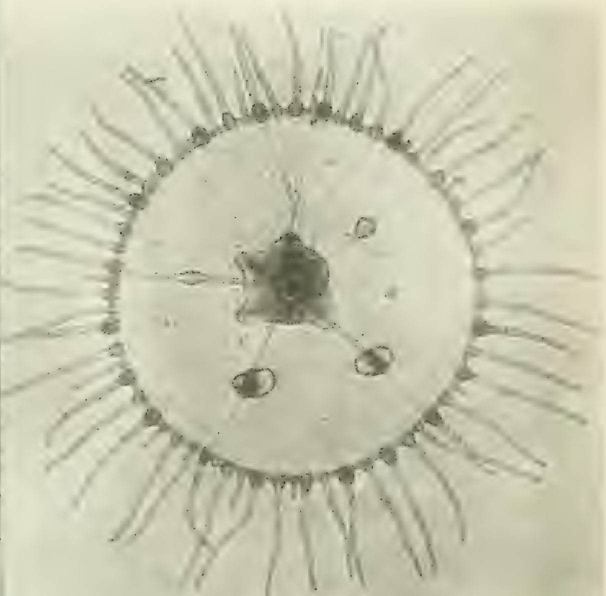

WOODWORT

ARTOTYPE, E. BIERSTADT, N. Y.

EUCOPE

PLATE

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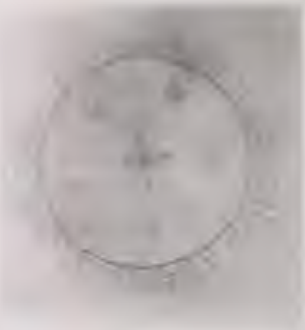

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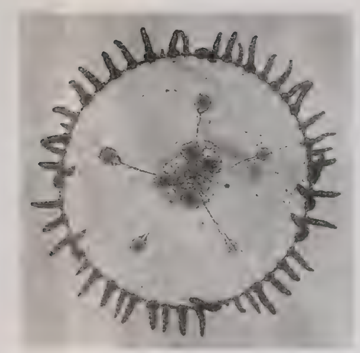

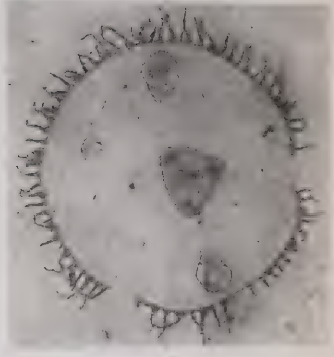

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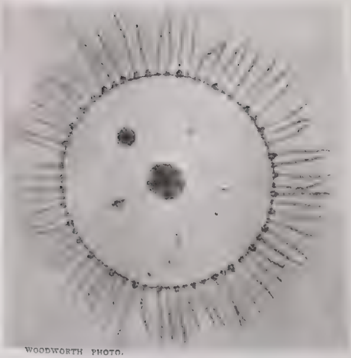

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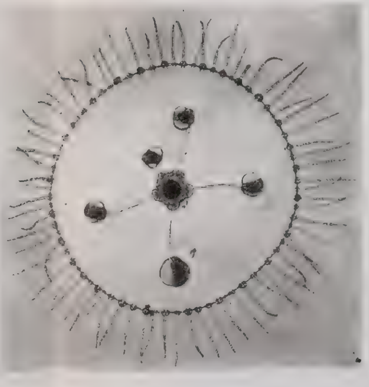

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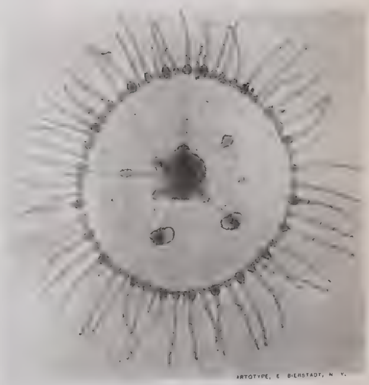

WOODWORTH PHOTO.

ARTOTYPE, E. BIERSTADT, N. Y.

PLATE V.

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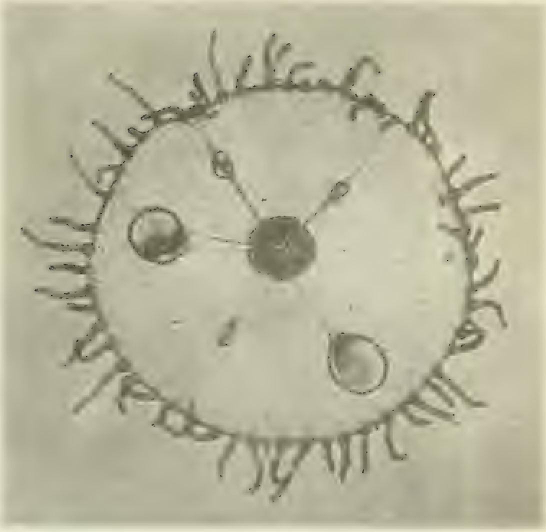

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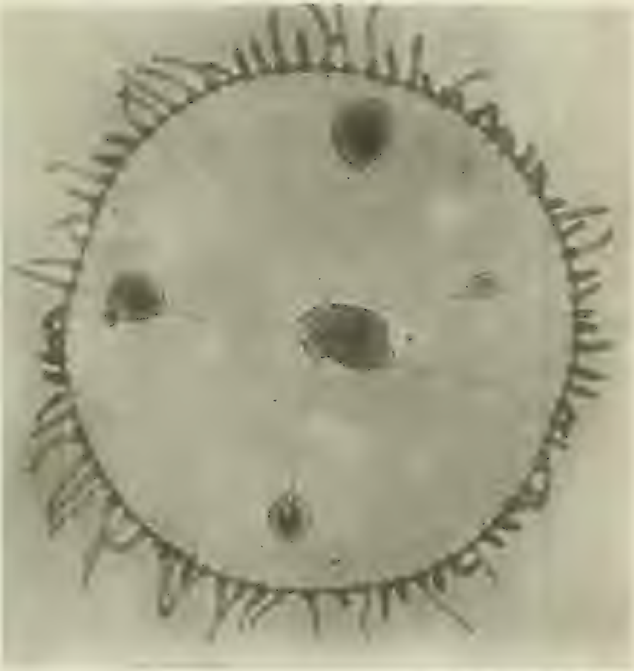

ARTOTYPE, E. BIERSTADT, N. Y.

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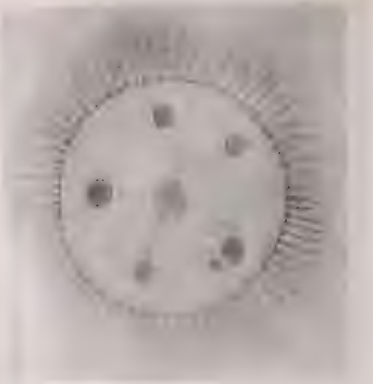

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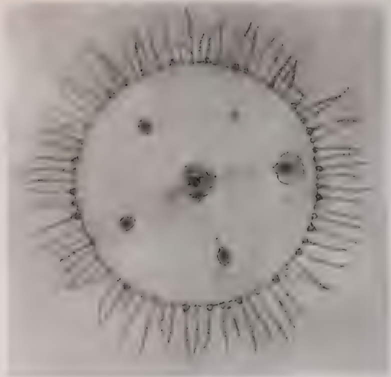

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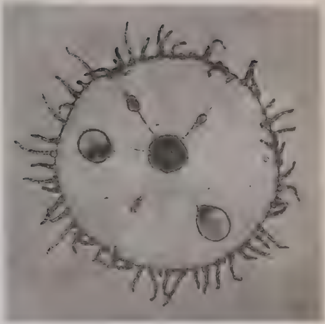

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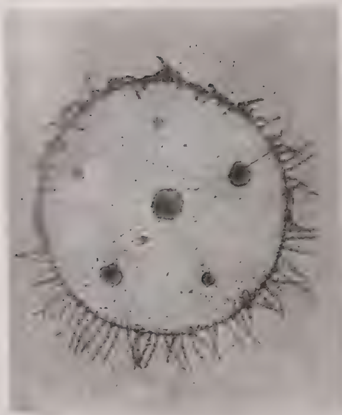

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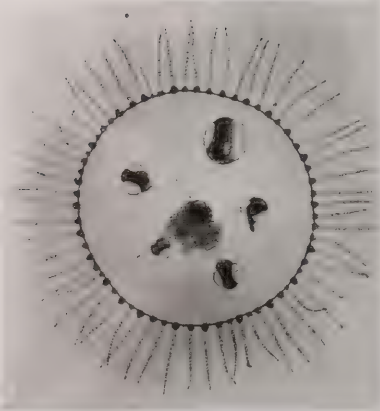

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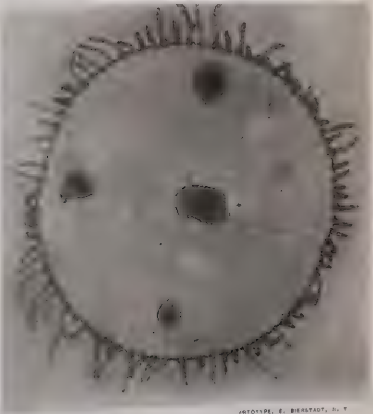

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ARTOTYPE, E. BIERSTADT, N. Y.

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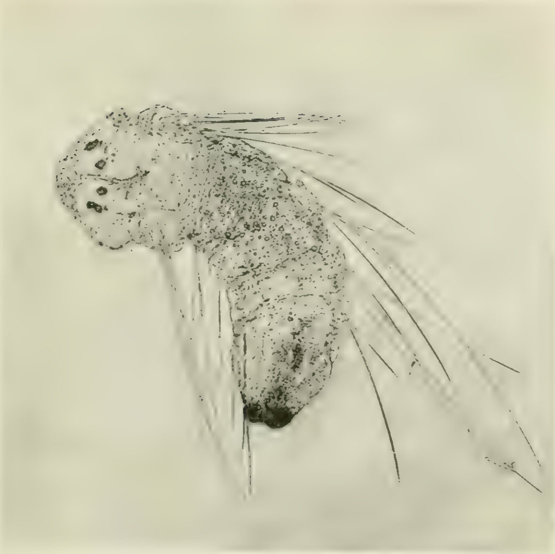

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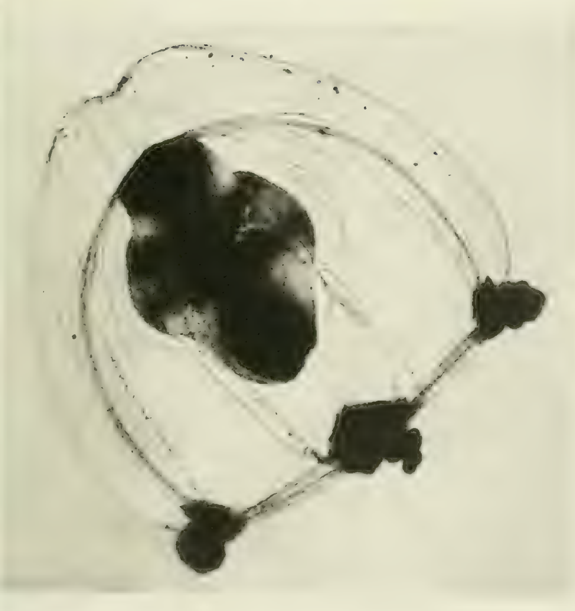

ARTOTYPE E. BIERSTADT, N. Y.

EUCOPE

PLATE VI.

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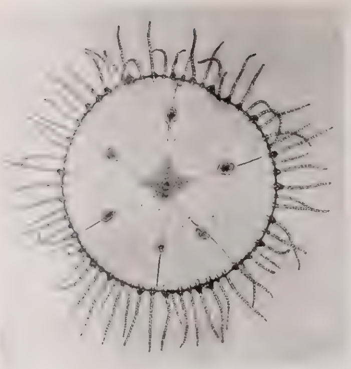

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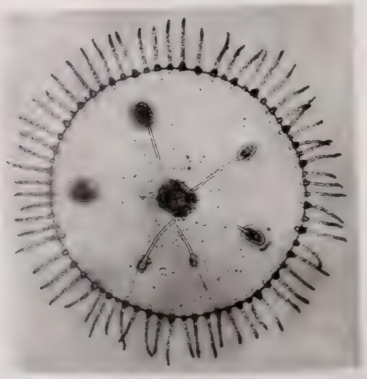

WOODWORTH PHOTO

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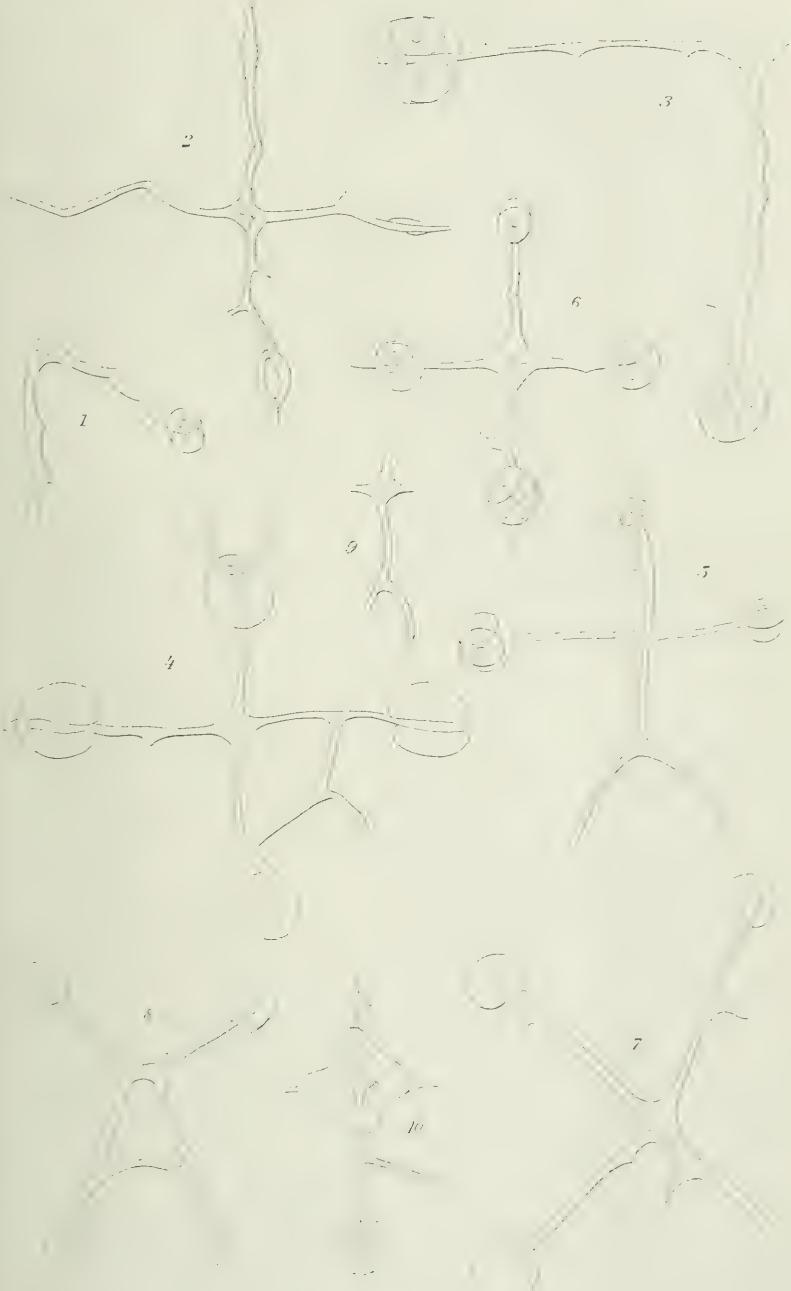
ARTOTYPE E. BIERSTADT, N. Y.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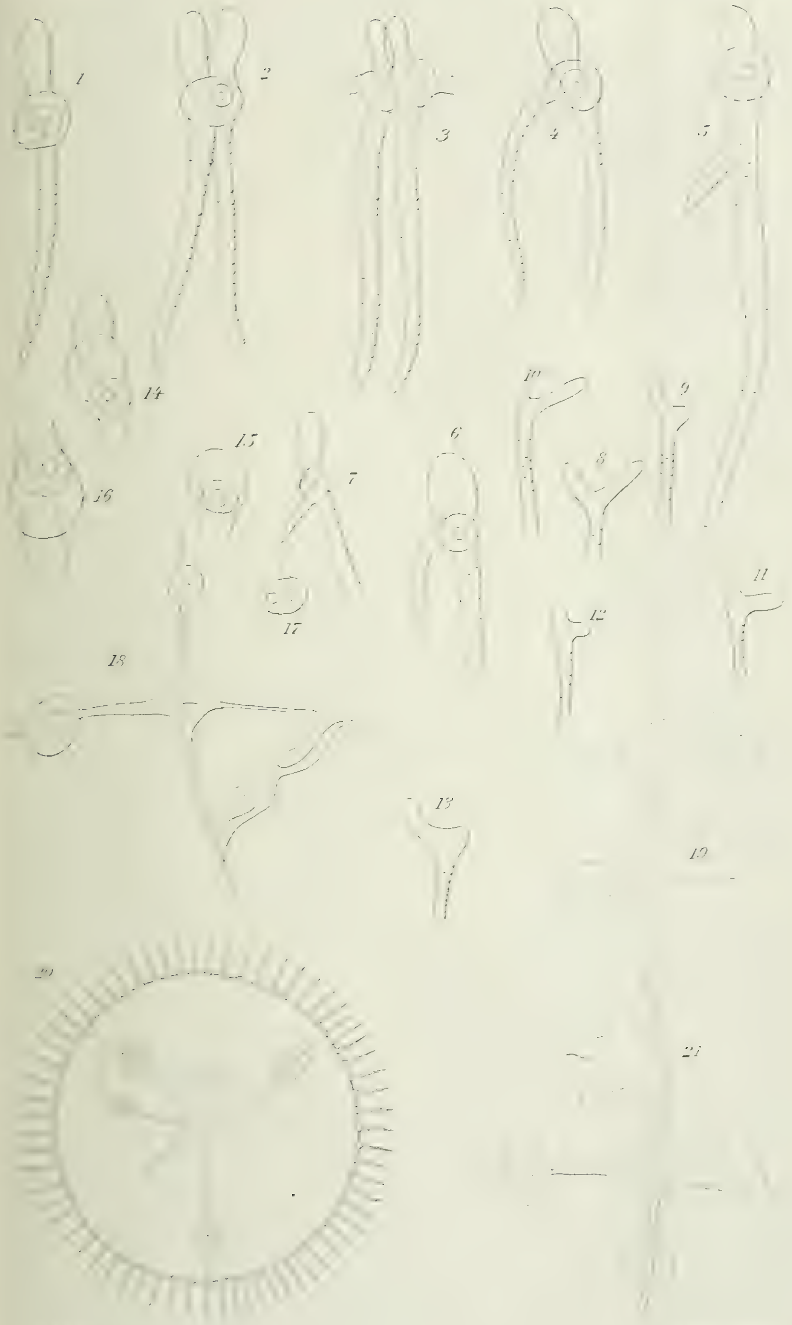

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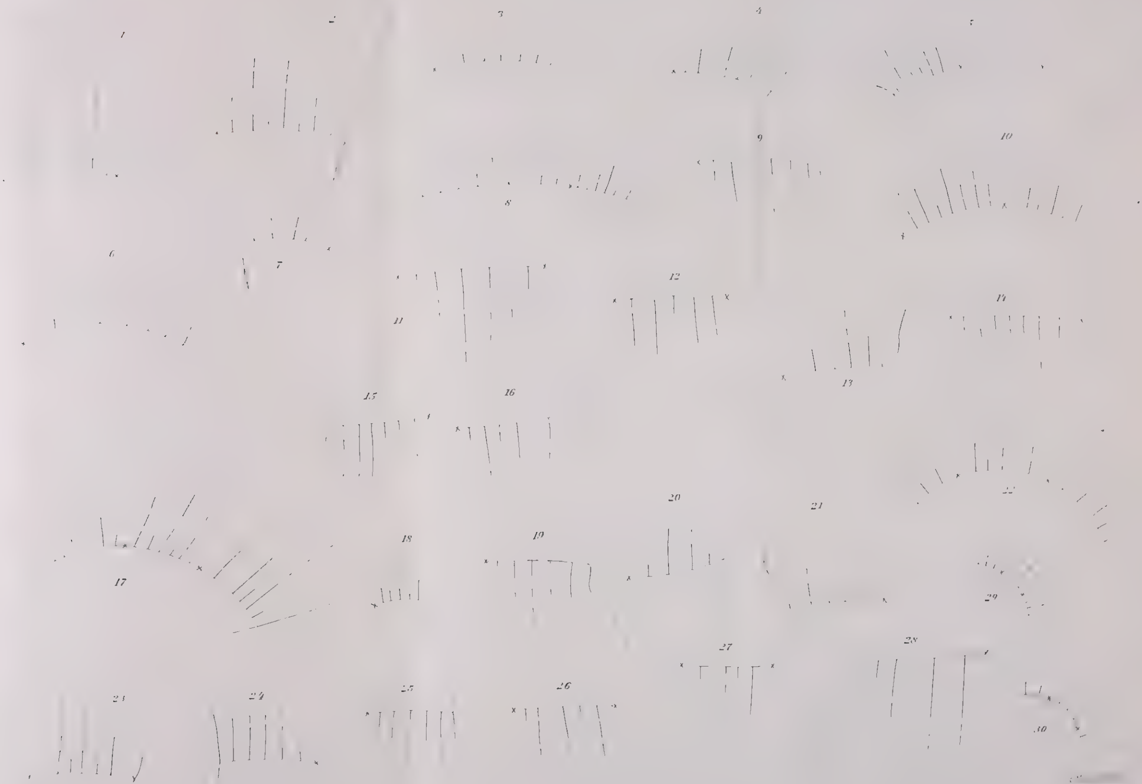

No. 3. — *Reports on the Results of Dredging, under the Supervision of* Alexander Agassiz, *in the Gulf of Mexico and the Caribbean Sea, and on the East Coast of the United States,* 1877 *to* 1880, *by the U. S. Coast Survey Steamer "Blake," Lieut.-Commander* C. D. Sigsbee, *U. S. N., and Commander* J. R. Bartlett, *U. S. N., Commanding.*

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XXXVII.

Supplementary Notes on the Crustacea. By Walter Faxon.

The following notes were made while identifying some of the "Blake" Crustacea that were retained as "duplicates" when the bulk of the collection was sent to A. Milne Edwards in Paris, and some (Macrura) that were returned by Milne Edwards undetermined. The notes chiefly consist of hitherto unpublished locality records, which add something to our knowledge of the distribution of many species. They also include descriptions of six new species (five Macrura and one Schizopod). Detailed lists of the dredging stations occupied by the "Blake" will be found in the Bulletin of the Museum of Comparative Zoölogy, Vol. VI. No. 1, and Vol. VIII. No. 4.

DECAPODA.

Anamathia hystrix (Stimps.).

Station 300. 82 fathoms. 1 ♂.

Anomalothir furcillatus (Stimps.).

Station 159. 196 fathoms. 1 ♀.
Off Port Royal, Jamaica. 100 fathoms. 1 ♀.

Pericera cornuta cælata (A. M. Edw.).

Station XX. 50 fathoms. 2 specimens.

Picroceroides tubularis Miers.

Station XXI. 33 fathoms. 1 ♂.

The rostral horns and preocular spines are longer than in the male specimen figured by Miers.

Lambrous pourtalesii Stimps.

Station XXX. 51 fathoms. 2 ♂.
" 133. 42 " 1 ♂.

Neptunus (Hellenus) spinicarpus (Stimps.).

Station 149. 60 to 150 fathoms. 1 ♀.

Achelous spinimanus (Latr.).

Station 144. 21 fathoms. 2 ♀.

Calappa flammea (Herbst).

Station 144. 21 fathoms. 1 ♂, 1 ♀.

Acanthocarpus alexandri Stimps.

Station 148. 208 fathoms. 1 ♂, 1 ♀.
" 149. 60 to 150 fathoms. 1 ♂.

Myropsis quinquespinosa Stimps.

Off Port Royal, Jamaica. 100 fathoms. 1 ♂.

Iliacantha subglobosa Stimps.

Station X. 103 fathoms. 1 ♀.

Cyclodorippe antennaria A. M. Edw.

Station 238. 127 fathoms. 1 ♀.
" 246. 154 " 2 ♀.
" 274. 209 " 1 ♂, 1 ♀.

Iconaxius caribbæus, sp. nov.

Plate I. Figs. 1-4.

Similar to *Iconaxius acutifrons* Bate, but different in the form of the rostrum, which is much broader than in *I. acutifrons*, less triangular in its outline, and broadly rounded at the anterior end; the upper border of the propodite of the larger cheliped, moreover, is entire, not denticulate as in *I. acutifrons*. The eyes are larger, and more heavily pigmented.

The margins of the rostrum are minutely denticulate, as in *I. acutifrons*, the median keel entire.

Length, 17 mm.

Station	166.	150 fathoms.	1 specimen.
"	232.	88 "	1 "
"	241.	163 "	3 "
"	283.	237 "	1 (type).

Lives as a commensal in Sponges of the genus *Farrea*.

The genus *Iconaxius*, of which four species have been previously described, has a wide distribution in the warm and temperate seas. It has been recorded from such remote localities as the Arabian Gulf, Banda Sea, Japan, Kermadec Islands, and the Gulf of Panama. It is now for the first time recorded from the Atlantic.

Polycheles crucifer (W.-S.).

Station	29.	955 fathoms.	3 specimens.
"	135.	450 "	1 "
"	179.	824 "	1 (exuviæ).
"	180.	982 "	1 specimen.
"	182.	1,131 "	1 "
"	188.	372 "	1 "
"	190.	542 "	1 "

Polycheles agassizii (A. M. Edw.).

Station	129.	314 fathoms.	3 specimens.
"	153.	303 "	1 "
"	238.	127 "	1 "
"	260.	291 "	1 "
"	XXVI.	297 "	1 "

Polycheles sculptus Smith.

Station	211.	357 fathoms.	3 specimens.
"	227.	573 "	1 "
"	230.	464 "	1 "

Station	245.	1,058	fathoms.	1	specimen.[1]
"	257.	553	"	2	"
"	265.	576	"	2	"
"	268.	955	"	1	"
"	VII.	610	"	1	"
"	XVIII.	600	"	2	"

Nephropsis agassizii A. M. Edw.

Nephropsis agassizii A. M. Edw., Ann. Sci. Nat., Zool., 6e sér., Vol. IX. No. 2, 1880.

Station	195.	502½	fathoms.	1 ♀.
"	200.	472	"	1 ♂.
"	227.	573	"	1 ♂.

Nephropsis aculeata Smith.

Nephropsis aculeata Smith, Proc. U. S. Nat. Mus., Vol. III. p. 431, 1881.
Nephropsis agassizii Smith, Bull. Mus. Comp. Zoöl., Vol. XV. p. 44, Fig. 240, 1888 (*nec* A. M. Edw.).
Nephropsis rosea (W.-Suhm MS.) Bate, Rep. "Challenger" Macrura, p. 178, Fig. 39, Pl. XXIII. Figs. 1, 2, Pl. XXIV. Fig. 1, 1888.

Station	185.	333	fathoms.	3	specimens.
"	188.	372	"	1	"
"	222.	422	"	3	"
"	226.	424	"	1	"
"	230.	464	"	1	"
"	?	?	"	1	"

There are two species of *Nephropsis* in the West Indian region, *N. agassizii* A. M. Edw., with two pairs of lateral spines on the rostrum, and *N. aculeata* Smith, with only one pair of rostral spines. *N. agassizii* was very inadequately described by A. Milne Edwards, and the type specimen, from the Strait of Florida, 1,500 metres, has never been returned to Cambridge. Soon after, the other species, *N. aculeata*, was described by Smith from specimens obtained off the south coast of New England, in 100 to 126 fathoms. Subsequently Smith and other authors supposed that *N. aculeata* was identical with *N. agassizii*. The chief differences between the two species are the following. In *N. agassizii* the rostrum is armed with two or two and a half pairs[2] of lateral teeth; in *N. aculeata* there is only one pair of lateral rostral spines;

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[1] Identified as *P. agassizii* by A. Milne Edwards, and so recorded by him in Bull. Mus. Comp. Zoöl., Vol. VIII. p. 66, 1880.

[2] The third lateral spine may occur on either the right or the left side of the rostrum.

the shell is less coarsely granulated, but more spiny in the former species than in the latter; the two lines on the proximal half of the rostrum in both species, widely diverging as they pass backward over the gastric area, are marked by small tubercles in *N. aculeata*, by distinct acute spines in *N. agassizii*; the top of the small median tubercle on the gastric area is truncated in *N. aculeata*, while in *N. agassizii* it is bluntly triangular, passing into a slight median longitudinal carina both in front and behind; the abdominal pleuræ are produced into longer spines in *N. agassizii* than in *N. aculeata*, and the spines moreover trend more distinctly backward, forming a stronger angle with the vertical axis of the pleura; the outer surfaces of these pleuræ are quite smooth in *N. agassizii*, while in *N. aculeata* they are conspicuously granulated both on their margins and on the distinctly raised central field; the lateral borders of the abdominal terga, which form a festoon on each side of the abdomen, are more strongly convex in the former species; another distinction is apparent in the sixth abdominal somite, viz. in *N. aculeata* the antero-lateral margin of the pleura is shorter than the postero-lateral border, whereas in the other species the antero-lateral border is longer than the postero-lateral; the tergum of this somite in *N. aculeata* sends off a granulated ridge from near its posterior lateral angles. — a ridge which runs forward into the upper, depressed portion of the pleura; this ridge is not found in *N. agassizii*.

Nephropsis rosea Bate is without much doubt a young individual of *N. aculeata*. *N. atlantica* Norman[1] is very similar to *N. agassizii*, but has a sharp spine on the anterior margin of the second abdominal pleura.

Stenopus hispidus (Oliv.).

Station	11.	37 fathoms.	1 specimen.
"	12.	36 "	1 "
"	36.	84 "	1 "
"	132.	115 "	2 "

Pontophilus gracilis Smith.

Station	43.	339 fathoms.	1 specimen.
"	47.	321 "	24 "
"	48.	533 "	1 "
"	221.	423 "	1 "

Prionocrangon pectinata, sp. nov.

Plate II. Figs. 4–7.

Rostrum spiniform, inclined at an angle of 45° to the axis of the body. Median dorsal line of the carapace armed with a row of eight spiniform teeth, which extends backward nearly to the posterior border of the carapace. Antero-lateral margins of the carapace angulated below the orbit. Telson much shorter than the appendages of the sixth abdominal somite, broad, with a pair of dorsal longitudinal ribs, abruptly contracted a short way beyond the middle; tip truncate, setiferous.

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[1] Proc Roy. Soc. Edinburgh for 1881–82, p. 684; Wood-Mason and Alcock, Ann. Mag. Nat. Hist., 6th Series, Vol. VII. p. 197, Fig. 4, 1891.

The eyes are absent; their peduncles are transformed into a pair of closely apposed trihedral processes, with acute and somewhat divergent tips. The first segment of the antennule is very long, reaching nearly to the end of the antennal scale; the second and third segments are, on the other hand, very short, the third bearing two flagella, the outer of which is very much shorter than the inner. The antennal scale is long and narrow, its outer margin lightly concave.

Length, 28 mm.

Station 201. Off Martinique. 565 fathoms. 1 ♀.

The rostrum is proportionally smaller than in *P. ommatosteres* Wood-Mason,[1] while the dorsal teeth of the carapace are larger, more numerous, and extend farther back on the cephalothorax; the telson is shorter; the antennal scale is longer than the proximal segment of the antennule. According to Wood-Mason, there is no trace of eyes or eye-stalks in *P. ommatosteres*. In *P. pectinata* there are distinct rudiments of the eye-stalks, as above described. *P. ommatosteres* comes from the Andaman Sea, 405 fathoms, and the Bay of Bengal, 200–350 fathoms.

Glyphocrangon aculeata A. M. Edw.

Station	29.	955	fathoms.	1	specimen.
"	163.	769	"	2	"
"	174.	878	"	1	"
"	190.	542	"	4	"
"	195.	502½	"	1	"
"	265.	576	"	2	"
"	VIII.	610	"	1	"

Glyphocrangon spinicauda A. M. Edw.

Station	148.	208	fathoms.	2	specimens.
"	274.	209	"	12	"
"	275.	218	"	6	"
"	281.	288	"	7	"

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[1] Ann. Mag. Nat. Hist., 6th ser., Vol. VIII. p. 362, 1891; Journ. Asiatic Soc. Bengal, Vol LXIII. p. 152, 1894; Ill. Zoöl. R. I. M. S. "Investigator," Crust., Pl. IX. Fig. 4, 1895.

Glyphocrangon nobilis A. M. Edw.[1]

Station	41.	860	fathoms.	6 specimens.
“	130.	451	“	2 “
“	162.	734	“	2 “
“	174.	878	“	4 “
“	176.	391	“	1 young.
“	179.	824	“	1 specimen.
“	185.	333	“	7 “
“	211.	357	“	1 young.
“	222.	422	“	2 “
“	227.	573	“	1 specimen.

Glyphocrangon neglecta, sp. nov.

Plate I. Figs. 5, 6.

Rostrum longer than the rest of the carapace, trending a little downward for the anterior half of its length, then curving gently upward to the tip, which is slender and acute; the anterior half of the rostrum is distinctly carinated in the median line, but the carina fades away before attaining the base of the rostrum;

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[1] The *Glyphocrangon* doubtfully referred to *G. nobilis* in my Report on the Stalk-eyed Crustacea of the “Albatross” Expedition of 1891 (Mem. Mus. Comp. Zoöl., Vol. XVIII. p. 142, 1895) is distinct from *G. nobilis*, as appears from an examination of a larger number of specimens of the latter species. In the “Albatross” species, which may be called *Glyphocrangon vicaria*, the upper surface of the rostrum is corrugated on each side of the median carina, in front of the anterior pair of lateral spines; in *G. nobilis* this corrugation does not exist. In *G. vicaria* the anterior moiety of the fourth or lateral crest of the carapace is broken into two parts by a deep notch; the part in front of the notch is produced anteriorly to form a strong spine, while the part behind the notch merely forms a projecting angle or shoulder; in *G. nobili* the anterior moiety of the fourth crest is continuous from the posterior end to the anterior spine. The tubercles of the first and second crests are more prominent and spiniform in *G. vicaria* than in *G. nobilis*. The dorsal carinæ of the telson are dentate anteriorly in *G. vicaria*, simple in *G. nobilis*. *G. vicaria* is even more closely related to *G. longirostris* Smith, which it represents on the Pacific side of the American continent. These are the chief differences between the two species: the rostrum, corrugated above in both species, is narrower in front of the anterior lateral spines in *G. vicaria* than in *G. longirostris*. The anterior moiety of the fourth lateral carina is broken into two distinct parts by a notch in the former, while it is merely sinuate in its outline in the latter. The tubercles on the first and second crests of the carapace are more prominent and spiny in the former than in the latter. The median dorsal crest of the abdomen, moreover, is more prominent. These differences, though very small, appear to be constant, and afford another instance of a slight divergence between two representative forms on the Atlantic and Pacific sides of the American continent. The type specimens of *G. vicaria* were dredged in 1189 fathoms, Lat. 0° 51′ N., Long. 91° 9′ W., “Albatross” Station 3411.

there are two pairs of lateral rostral spines, one of which lies in advance of the eyes, the other just behind the posterior wall of the orbit; on the lower face of the rostrum there appears just the slightest trace of a median longitudinal carina. The upper surface of the first or dorsal pair of carinæ is eroded; behind the cervical groove this pair of carinæ converge towards one another. Just in front of this pair of carinæ, lying in the median line at the base of the rostrum, is a small tubercle or papilla. In the interval between the first and second carinæ on each side are about four faint tubercles on the cardiac region, and on each side of the gastric region are four larger low tubercles, the hindmost of which is the largest of all. The anterior moiety of the third carina (adopting Wood-Mason's terminology) is well developed as a backward prolongation of the external orbital spine, which is long, acute, and inclined outward and upward. The fourth carina is also developed both anteriorly and posteriorly to the cervical groove, its anterior moiety being continuous with the antero-inferior, or branchiostegian, spine of the carapace. Barring the external orbital and branchiostegian spines, the anterior moieties of both the third and fourth carinæ are entire, without a trace of spine or tooth. The trend of the branchiostegian spine is nearly straight forward, its downward and outward deflection being very slight. With the exceptions noted above, the spaces between the carinæ of the carapace are pretty smooth.

The abdomen is lightly sculptured for the genus to which this species belongs. Only the first and sixth segments are conspicuously carinated above. The pleuræ of the second abdominal segment are one-toothed. The telson exceeds the last pair of abdominal appendages, and is rather abruptly bent upward at the tip.

Length, 75 mm.; cephalothorax including rostrum, 35 mm.; rostrum, 19 mm.; telson, 13 mm.

Station 261, off Grenada.	340 fathoms.	1 ♀ with eggs.	Type.
" 153, off Montserrat.	303 "	1 ♂.	
" 260, off Grenada.	291 "	1 young.	

This species is peculiar in having the anterior moiety of the third and fourth carinæ of the carapace well developed and continuous with the external orbital and branchiostegian spines respectively. In *G. gilesii* Wood-Mason, which also has the anterior portion of both the third and fourth crests developed, these crests are produced anteriorly into small spines independent of the external orbital and branchiostegian spines.

Stylodactylus serratus A. M. Edw.

Station 205.	334 fathoms.	3 specimens.
" 151.	356 "	1 "

Pantomus parvulus A. M. Edw.

Station 134 248 fathoms. 2 specimens.

Pandalus longipes A. M. Edw.

Station	274.	209 fathoms.	12+ specimens.
"	291.	200 "	12+ "
"	295.	180 "	2 "
"	300.	82 "	12+ "

Pandalus ensis A. M. Edw.

Station	208.	213 fathoms.	1 specimen.
"	258.	159 "	2 "

Pandalus leptocerus Smith.

Station 345. 71 fathoms. 1 specimen.

Heterocarpus lævis A. M. Edw.

Station XXVI. 297 fathoms. 1 specimen.

Heterocarpus alexandri A. M. Edw.

Station 196. 1030 fathoms. 1 specimen.

Heterocarpus ensifer A. M. Edw.

Station	146.	245 fathoms.	1 specimen.
"	153.	303 "	1 "
"	258.	159 "	2 "

Nematocarcinus cursor A. M. Edw.

Station	151.	356 fathoms.	12+ specimens.
"	160.	393 "	2 "
"	161.	583 "	1 "
"	205.	334 "	2 "
"	227.	573 "	2 "
"	274.	209 "	1 "

Hoplophorus gracilirostris A. M. Edw.

Station	100.	250–400 fathoms.	1 specimen.
"	191.	108–250 "	1 "
"	226.	424 "	1 "
"	230.	464 "	1 "
"	258.	159 "	1 "
"	271.	458 "	1 "

Acanthephyra affinis, sp. nov.

Plate II. Fig. 1-3.

Similar to *Acanthephyra (Systellaspis) lanceocaudata* Bate, but different in the following regards: the apical tooth of the antennal scale projects forward far beyond the membranous part of the organ; the telson is shorter than even the inner branches of the posterior pair of abdominal appendages, and its dorsal surface is flattened, but not grooved.

The seven teeth that surmount the gastric crest are closely approximated, and increase in size successively from the first to the fifth. The sixth is about equal to the fifth, the seventh a little smaller. The egg of this species measures 3 × 2 mm.

Length, 100 mm.

Station 258. 159 fathoms. 1 ♀.

This species belongs to the subgenus *Systellaspis*, in which the orbit is continuous to the first antennal tooth (the orbital tooth being absent), the dorsal carina of the sixth abdominal somite is wanting, and a prominent angle or tooth projects from each side of the anterior border of the first abdominal somite, overlapping the posterior margin of the carapace. The eggs, moreover, are of large size, indicating a protracted period of intra-oval development.

Acanthephyra debilis A. M. Edw.

Station 107. 428 fathoms. 1 specimen.

Acanthephyra armata A. M. Edw.

Station 135. 450 fathoms. 1 specimen.
" 151. 356 " 2 "

Sicyonia edwardsii Miers.

Station 142. 27 fathoms. 1 specimen.

Sicyonia brevirostris Stimps.

Station 38. 20 fathoms. 1 specimen.

Peneus brasiliensis Latr.

Station 37. 35 fathoms. 2 specimens.
" 29. 955 " 3 young.

Parapeneus megalops Smith.

Station	147.	250	fathoms.	4	specimens.
“	148.	208	“	4	“
“	258.	159	“	6	“
“	275.	218	“	4	“
“	281.	288	“	10	“
“	283.	237	“	1	“

Parapeneus politus Smith.

Station 36. 84 fathoms. 27 specimens.

Haliporus debilis (Smith).

Station 47. 321 fathoms. 1 specimen.

Plesiopeneus armatus (Bate).

Station	31.	1,920	fathoms.	2	specimens.
“	187.	411	“	1	“

Hemipeneus triton Fax.

Station 227. 573 fathoms. 1 specimen.

Benthesicymus bartletti Smith.

Station	29.	955	fathoms.	1	specimen.
“	33.	1400–1568	“	1	“
“	163.	769–878	“	2	“
“	179.	824	“	1	“
“	190.	542	“	1	“
“	227.	573	“	2	“
“	245.	1058	“	1	“
“	265.	576	“	1	“
“	288.	399	“	2	“

Sergestes robustus Smith.

Station	205.	334	fathoms.	1	specimen.
“	211.	357	“	1	“
“	260.	291	“	1	“
“	264.	416	“	1	“
“	265.	576	“	2	“
“	267.	626	“	1	“

Sergestes mollis Smith.

Station 30. 968 fathoms. 2 specimens.

SCHIZOPODA.

Lophogaster longirostris, sp. nov.

Plate. II. Figs. 8-10.

Similar to *L. typicus* Sars, but different in the great length of the median spine of the rostrum, which far surpasses the antennular peduncle, and almost attains to the tips of the antennal scales. There are six teeth along the outer edge of the antennal scale. Length, 27 mm.

Station 50. 119 fathoms. 20 specimens.

Gnathophausia zoëa W.-Suhm.

Station	185.	333	fathoms.	2	specimens.
"	201.	565	"	1	"
"	221.	423	"	1	"
"	227.	573	"	1	"
"	228.	785.	"	1	"
"	230.	464	"	1	"
"	284.	347	"	2	"
"	288.	399	"	3	"

Eucopia sculpticauda Fax.

Station 30. 968 fathoms. 1 specimen.

Petalophthalmus armiger W.-Suhm.

Station 29. 955 fathoms. 1 ♀.

This is the specimen figured in my Report on the Stalk-eyed Crustacea of the "Albatross" Expedition of 1891, Pl. LIII. Fig. 2 (Mem. Mus. Comp. Zoöl., Vol. XVIII.).

STOMATOPODA.

Squilla empusa Say.

Station 36. 84 fathoms. 1 specimen (young).

Pseudosquilla ciliata (Fabr.).

Martinique. 1 specimen.

ISOPODA.

Bathynomus giganteus A. M. Edw.

Station 179. 824 fathoms. 1 specimen, 157 × 80 mm.
" VII. 610 " 1 " 107 × 49 "

According to Wood-Mason and Alcock (Ann. Mag. Nat. Hist., 6th Series, Vol. VII. p. 270, 1891), this remarkable Isopod was captured in the Bay of Bengal at a depth of 740 fathoms. Dr. Arnold Ortmann[1] has described a second species of *Bathynomus* (*B. dœderleini*), taken on the coast of Japan, near Enoshima, Sagarni Bay. The depth is not recorded.

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[1] Proc. Acad. Nat. Sci. Phila., 1894, p. 191.

EXPLANATION OF THE PLATES.

PLATE I.

Fig. 1. *Iconaxius caribbæus* Fax. M. C. Z., No. 4195. Blake Sta. 283. × $5\frac{1}{3}$.

Fig. 2. The same. Head, from above. × $5\frac{1}{3}$.

Fig. 3. The same. Right chela, from the outside. × $5\frac{1}{3}$.

Fig. 4. *Iconaxius caribbæus* Fax. Telson and posterior pair of appendages. M. C. Z., No. 4147. Blake Sta. 241. Much enlarged.

Fig. 5. *Glyphocrangon neglecta* Fax. Female, dorsal view. M. C. Z., No. 4434. Blake Sta. 261. × $1\frac{1}{3}$.

Fig. 6. The same. Lateral view. × $1\frac{1}{3}$.

PLATE II.

Fig. 1. *Acanthephyra affinis* Fax. Female. M. C. Z., No. 4410. Blake Sta. 258. × $1\frac{1}{3}$.

Fig. 2. The same. Telson. × $1\frac{1}{3}$.

Fig. 3. The same. Antennal scale. × $1\frac{1}{3}$.

Fig. 4. *Prionocrangon pectinata* Fax. Female. M. C. Z., No. 4436. Blake Sta. 201. × 4.

Fig. 5. The same. Carapace, from above. × 4.

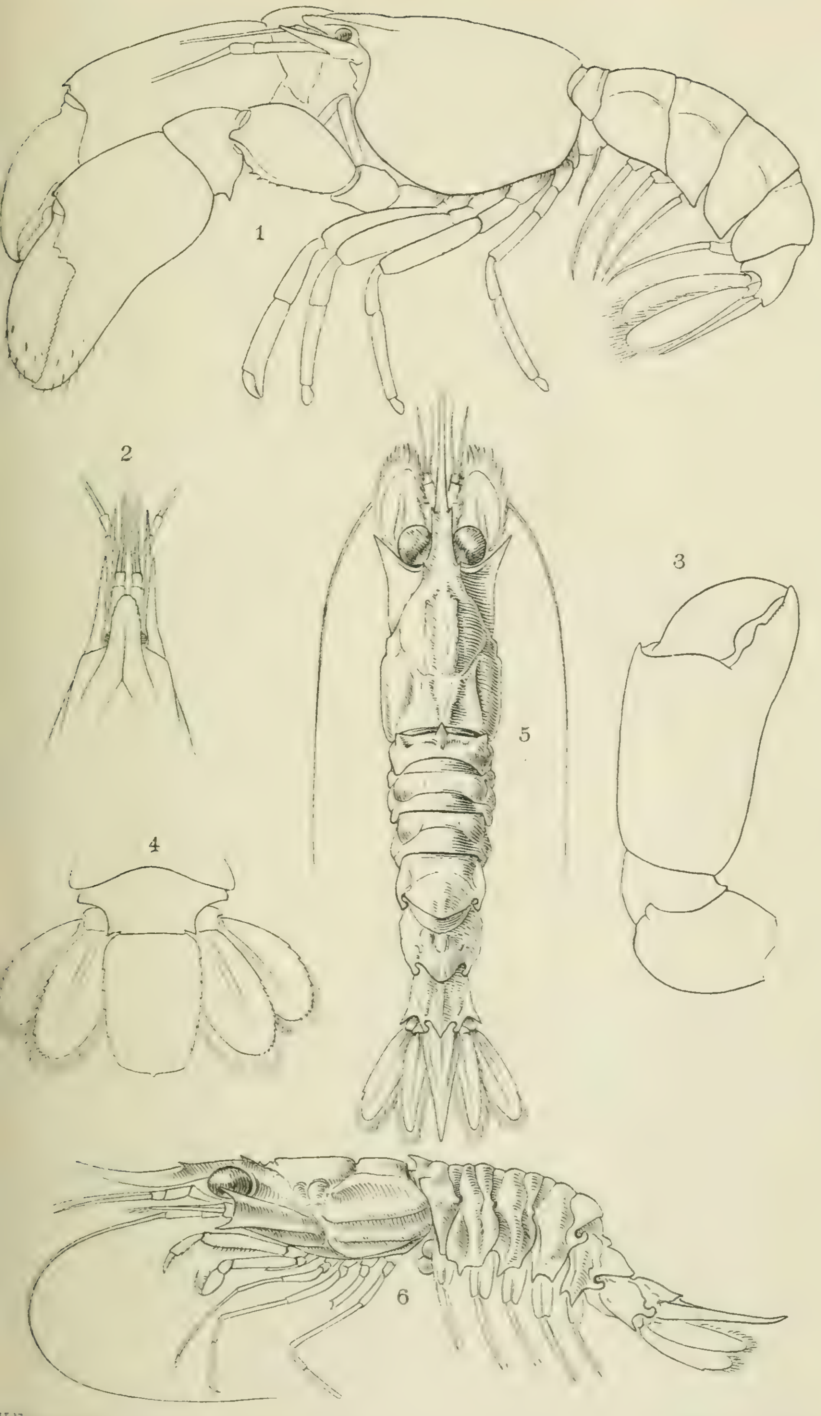
Fig. 6. The same. Chela. × 4.

Fig. 7. The same. Telson and posterior pair of abdominal appendages. × 4.

Fig. 8. *Lophogaster longirostris* Fax. M. C. Z., No. 4380. Blake Sta. 50. × 4.

Fig. 9. The same. Carapace, from above. × 4.

Fig. 10. The same. Telson and posterior pair of abdominal appendages. × 4.



H.Emerton del.

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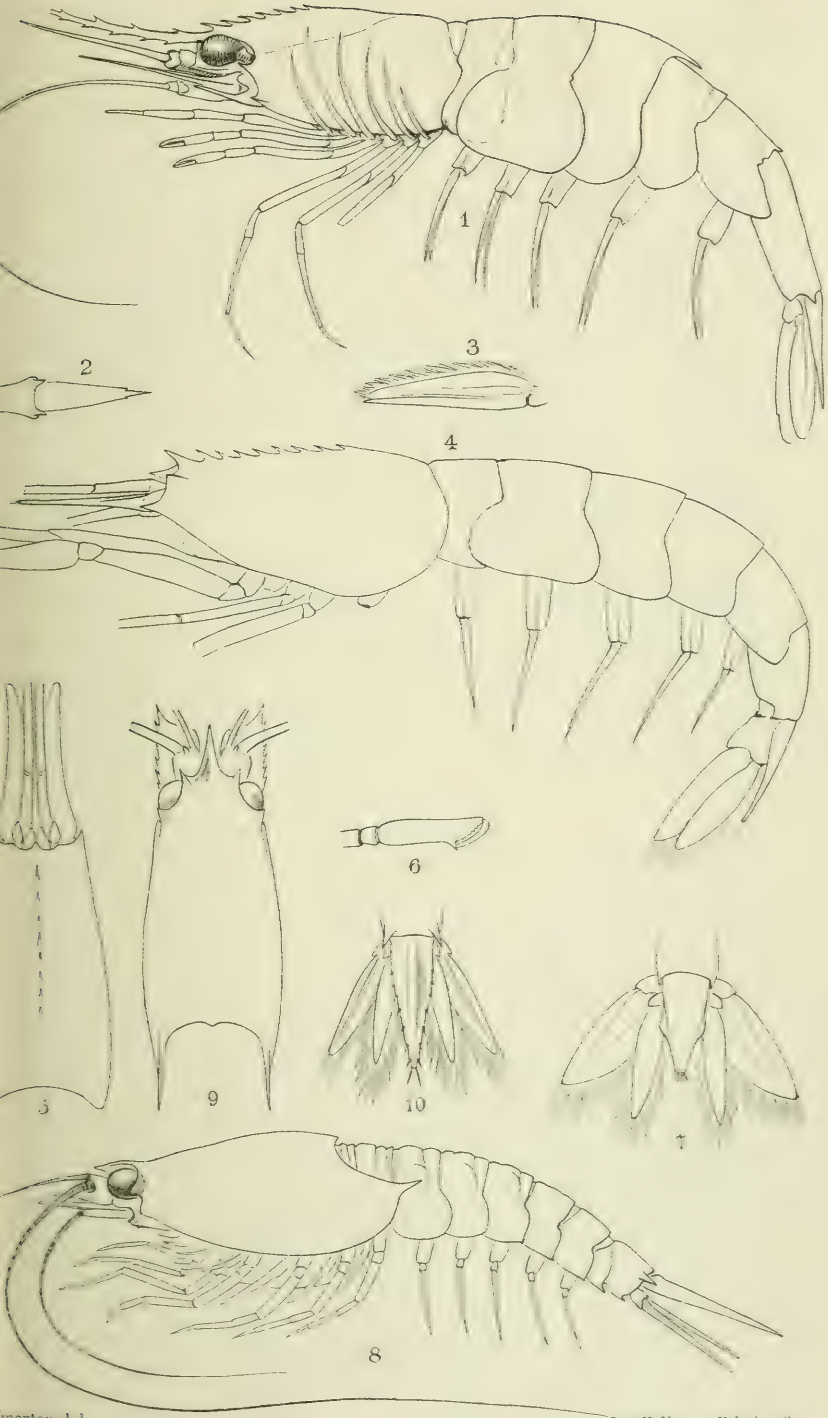
1–4 Iconaxius caribbæus Fax.
5–6 Glyphocrangon neglecta Fax.



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1-3 Acanthephyra affinis Fax.
4-7 Prionocrangon pectinata Fax.
8-10 Lophogaster longirostris Fax.

No. 4.—*On the Color and Color-Patterns of Moths and Butterflies.*[1]

By Alfred Goldsborough Mayer.

This research is an investigation of the general phenomena of Color in Lepidoptera, and also a special account of the Color-Patterns of the Danaoid and Acraeoid Heliconidae, and of the Papilios of Tropical South America, and has been carried out under the direction of my friend and instructor, Dr. Charles B. Davenport; and the work was done in connection with one of the courses given by him in Harvard University in 1894–95.[2] I am indebted to Dr. Davenport not only for suggesting the subject, but also for his kindness in devoting much time to a criticism of the results.

The paper is divided into three parts. Part A contains an account of the general phenomena of color in Lepidoptera; Part B is devoted to a special discussion of the color-variations in the Heliconidae, with special reference to the phenomena of mimicry; and Part C consists of a summary of those results which are believed to be new to science. A Table of Contents is given at the end of the paper.

PART A.

GENERAL PHENOMENA OF COLOR IN LEPIDOPTERA.

I. Classification of Colors.

We follow Poulton ('90) in dividing Lepidopterous colors into (1) pigmental and (2) structural.

(1) *Pigmental Colors* are due to the presence of an actual pigment within the scales, and although such colors are very common in the Lepidoptera, it is frequently very difficult to say off-hand whether a given color is due to a pigment or to some structural effect. Coste ('90–'91) and Urech ('93) have, however, given criteria for determining whether a color is due to a pigment or to some other cause. They succeeded, for example, in dissolving out the color in many

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXIV.

[2] This paper was written in 1895 essentially as it now stands.

cases, leaving the wing white or colorless. Coste used as solvents a number of strong acids and alkalis; while Urech confined himself to the use of water, hydrochloric acid, and nitric acid. Their results may be conveniently summarized as follows:—

Black according to Urech is a pigmental color, for it may be dissolved out of the wings by means of hydrochloric or nitric acid.

Brown is usually insoluble in water, but is soluble in hydrochloric or nitric acid.

The *red and orange* pigments of the Pieridae, Lycaenidae, Nymphalidae, Zygaenidae, and some Papilios are soluble in water. They are insoluble in water in the Sphingidae, Arctidae, Bombycidae, Saturnidae, and Geometridae.

Yellow pigment is acted upon by reagents in almost the same way as the red and orange, especially if both red and yellow appear upon the same wing. It is soluble in the Pieridae, Lycaenidae, Nymphalidae, Satyridae, and some Papilios, but insoluble in the Sphingidae, Arctidae, Geometridae, and a few Noctuidae.

White is usually a structural color, but can be dissolved out from the wings of the Pieridae by water, being in this case, of course, due to a pigment.

Green pigment can be dissolved out by water in the cases of the Pieridae, Lycaenidae, and Geometridae. In the vast majority of cases, however, it is a structural color.

Violet and blue are almost always due to structural causes. In a few cases, however, as in Smerinthus ocellatus, a blue pigment can be dissolved out.

We see, then, that black, brown, red, orange, and yellow are usually due to pigment, while white, green, violet, and blue are generally due to structural effects.

It is well known that the scales of Lepidoptera are essentially hollow, flattened sacs often inclosing pigment, and Burmeister ('78) arrives at the conclusion, from a study of the scales in various species of Castnia, that the pigment is for the most part attached to the upper layer of the scale-sac, rendering it opaque, while the lower layer receives less pigment and is, in consequence, a little more translucent.

(2) *Structural Colors* owe their origin to the external structure of the scales or wing-membranes and not to the presence of a pigment. They are often caused by diffraction, due to the scales being covered with fine, parallel striae. Some of the most splendid colors in the

animal kingdom are due to this cause; such are the iridescent and opalescent hues of many of the Morphos and Indo-Asiatic Papilios. Very often the scales which display such brilliant colors contain no pigment whatsoever; for if one will merely soak them in alcohol, ether, or water, all color disappears, and the scales become as transparent as glass. This test was devised by Dimmock ('83), who used it upon the brilliantly colored scales of many beetles. It was first discovered by Burgess ('80), and has since been confirmed by Kellogg ('94), that the striae which produce these structural colors are all upon the outer surface of the scale, *i. e.*, the surface which is away from the wing-membrane and exposed to the light. Kellogg ('94) has determined the distance apart of the striae upon the scales of many species of Lepidoptera. It appears, for example, that the striae upon the scales of Danais plexippus are 2μ apart, those upon the transparent scales of Morpho sp. 1.5μ, upon the pigment-bearing scales of Morpho 0.72μ, and upon Callidryas eubule 0.9μ apart. It is very evident, then, that the brilliant coloration of the scales may be due to this fine striation, for the striae upon Rowland's or Rutherfurd's finest gratings are approximately 1.5μ apart, which is about the average distance between the ridges of the scales.

Structural colors are, however, not always due to diffraction; in the case of white, for example, the color is almost invariably due to a reflection of all, or nearly all, the light that impinges upon the scales. As long ago as 1855 Leydig pointed out that the silvery white color seen in the scales of some spiders, such as Salticus and Tegenaria, was due to air contained within them; and more recently Dimmock ('83) has shown that silvery white and milk-white colorations are due to optical effects produced by reflected light. In the silvery white scales, however, such as those of the under surface of the hind wings of Argynnis, there must be a polished reflecting surface toward the observer, for both silvery and milk-white colors appear simply milk-white by reflected light.

(3) *Combination Colors* owe their richness and brilliancy to a combination of structural and pigmental effects. The geranium-red spots upon the hind wings of the Mexican Papilio zeunis Lucas owe their red color to pigment, but over this red there plays, in certain lights, a beautiful pearly iridescence, which, in combination with the red, greatly enhances its charm. Urech ('92) has demonstrated that in the Vanessas there are scales which have chemical coloring matter

and interference colors also. In addition, he points out the interesting case of certain Lycaenidae where the scales exhibit to the eye only interference effects, and yet a pigment can be dissolved out of them by the use of water.

(4) *Quantitative Determination of Pigmental Colors.* I have analyzed the colors of many butterflies by means of the spectroscope, and also by Maxwell's discs. As is well known, Maxwell's discs are colored circular discs of cardboard, perforated at the center and slit along a radius so that two or more of them may be slid over each other, thus exposing different proportions of each. Then by rapidly rotating them the colors become blended, and thus it becomes possible to match any color, and to discover its fundamental constituents. By this means I have determined that the vast majority of the colors found in Lepidoptera are impure; that is to say, they contain a large percentage of black.

For example the white of the upper surface of the wings of the common Pieris rapae consists of: 17% black, 13% emerald-green, 10% lemon-yellow, and 60% white.

Also the so-called "blacks" found in butterflies are rarely jet-black, but, almost always, only deep shades of brown. For instance the deep brown color of the under surface of the wings of Heliconius melpomene consists of 93% black, 3% lemon-yellow, 3.5% of Maxwell's fundamental red (vermilion), and 0.5% of von Bezold's fundamental blue-violet.

The purest color I have met with is the canary-yellow ground color of the wings of Papilio turnus, which seems to consist of white light with the addition of a little yellow.

Other colors all possess considerable black. Thus the glaucous green of Colaenis dido consists of black 29%, vermilion 24%, emerald-green 37%, von Bezold's blue-violet 10%.

The sepia-brown ground color of Cercyonis alope consists of black 71%, vermilion 21.5%, emerald-green 7.5%.

The tawny rufous color of the wings of Mechanitis polymnia, etc., is made up of black 46%, vermilion 40%, lemon-yellow 14%.

The rufous red patch on the upper surface of the fore wings of Heliconius melpomene is made up of black 27%, vermilion 66.5%, lemon-yellow 6.5%.

The yellow of the fore wings of Mechanitis polymnia consists of lemon-yellow 67%, emerald-green 14%, and white 19%.

(5) *Spectrum Analysis of Colors of Lepidoptera.* I have made some spectrum analyses of the light reflected from the wings of various butterflies, by means of a piece of apparatus most kindly suggested for the purpose by Prof. Ogden N. Rood of Columbia College. The arrangement is shown in Figs. 1, 2, Plate **1**; Fig. 1 being a perspective view, and Fig. 2 a horizontal section of the apparatus, which consists of a rectangular box, blackened upon the inside, and having a well-fitting cover. A rectangular slit (O) was cut through one of the long sides of the box, near one end, and the other end of the same side was perforated in order to allow the admission of the direct-vision spectroscope (S). Imagine that we wish to examine the yellow spots from a butterfly's wing. All of the yellow spots from the wing are cut out, and pasted upon two pieces of cardboard so as to make two large unbroken patches of color. The pieces of cardboard are then blackened upon all those places where the colored wing was not pasted. One of the cardboards is then suitably mounted upon the back of the box at B; the other is placed upon a vertical support (F), the plane of which is parallel to the back of the box.

The working of the apparatus is as follows: the sunlight enters by the slit (O) and is reflected and diffused three or four times between the pieces of colored wing mounted upon the back (B) of the box, and the vertical support (F). The manner of this reflection and diffusion is shown by the dotted lines of Fig. 2. After undergoing several reflections, the light enters the direct-vision spectroscope (S). The slit of the spectroscope is wide open, and thus the light which enters it may readily be examined. It was found that it was necessary that the light be reflected more than once from the wing before it enters the spectroscope, for the first reflection shows so much white light that it is usually quite impossible to analyze the true color of the wing, the predominant colors being obscured by a continuous spectrum. In general it was found that the colors of the wings are not simple, but compound; that is to say, they are made up of a mixture of several different colors.

For example, the spectrum of the rufous ground color of the upper surface of the wings of Danais plexippus consists of all of the red and yellow of the spectrum and about 75% of the green.

The red spots upon the upper side of the fore wings of Heliconius melpomene also consist of the red and yellow and a very faint, hardly visible, trace of green.

The glaucous green patches on the wings of Colaenis dido are composed mainly of green and yellow, but there is also a faint development of about half of the blue and a still fainter trace of red.

The iridescent blue-green ground color of the upper surface of the wings of Morpho menelaus, viewed in such a way that the light makes an angle of about 20° with the normal to the surface of the wing, gives a spectrum of green and blue about equally developed.

The yellow ground color found on the upper side of the wings of Papilio turnus shows a continuous spectrum, in which the yellow seems to be rather more brilliant than in the normal spectrum of white light.

The sepia-brown ground color of the upper surface of the wings of Cercyonis alope gives a spectrum which lacks only the blue-green and blue.

(6) *Summary of Results.* The researches of Coste ('90–'91) and Urech ('93) have demonstrated that the colors of butterflies and moths may be produced by two causes: by the presence of an actual pigment, or by some structural effect. Some colors are due entirely to pigment, others to structural causes, and still others to a combination of the two.

Black, brown, red, orange, and yellow are invariably due to pigment.

Green is usually due to a structural effect, but in a few cases there is a green pigment present.

White, blue, and violet are almost invariably due to structural causes.

In addition to these facts I have found that most of the colors which are displayed by Lepidoptera contain a surprisingly large percentage of black. Also they are usually not simple colors, but composed of a mixture of several different colors. It is remarkable that Natural Selection, which is generally assumed to have been one of the principal factors in bringing about the wonderful development of colors in Lepidoptera, has not been potent enough to make these colors purer than is the case in existing butterflies.

II. The essential Nature of Pigmental Color in Lepidoptera.

(1) *Pigments of Larvae.* Poulton ('85) showed that the phytophagous larvae of Lepidoptera "owe their colour and markings to

two causes: (1) Pigments derived from their food-plants, chlorophyll and xanthophyll, and probably others; (2) pigments proper to the larvae, or larval tissues made use of because of some (merely incidental) aid which they lend to the colouring, *e. g.* fat." Poulton concludes that all green coloration is due to chlorophyll, and that nearly all yellows are due to xanthophyll. All other colors, including black and white and some yellows, are due to pigments proper to the larvae themselves.

Later, in 1893, Poulton proved that the larvae of Tryphaena pronuba could transform both etiolin and chlorophyll into a larval coloring matter, which may be either green or brown. It thus appears that some brown pigments are derived from food, and are merely modified plant pigments. Green larvae have green blood, and this color is due to chlorophyll in solution. It is remarkable that this chlorophyll solution is stable under the prolonged action of light, and in this respect is different from any other known solution of chlorophyll. It is worthy of note, further, that the spectrum of this green blood shows a great resemblance to that of chlorophyll. "In fact the two spectra are far nearer to one another than the ordinary spectrum of chlorophyll in alcoholic solution, is to the unaltered chlorophyll of leaves."

(2) *Pigments of Imagines.* In 1891, Urech showed that the similarity between the color of the urine of butterflies and the principal color of their scales is so close that it cannot be considered as accidental, but rather must be regarded as physiological. Urech compares in a table the color of the urine and that of the scales of 29 species of Lepidoptera. In all but two species the resemblance is very close.[1]

Urech further shows that the color of the urine (and the corresponding color of the scales) is not dependent upon the kind of food, for one and the same food plant may be differently digested in different groups of Lepidoptera. Thus he compares the behavior of a Vanessa with that of one of the Microlepidoptera (leaf-rollers). Both of these feed upon the nettle (Urtica). In the larva of the Vanessa the contents of the stomach are intensely green, but become red in the pupa. In the case of the leaf-roller the contents of the stomach are never markedly green and become insipid in color during the pupal stage.

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[1] Likewise, Hopkins ('94) has shown that in the Pieridae the urine is tinged by a yellow substance having exactly the color of the wings.

Poulton has shown that the reddish fluid voided by the Vanessas immediately after emergence from the chrysalis contains uric acid, and Hopkins ('94) says that when the yellow Pieridae emerge, they often void from the rectum a large quantity of uric acid. It should be borne in mind however, as Urech himself suggests, that the pigment found within the wings may not be identical in chemical composition with the similarly colored fluid from the alimentary tract.

Hopkins ('89, '91, '94, '96) has discovered that the white pigment found in the scales of Pieridae is uric acid, and that the red and yellow pigments of the Pieridae are due to derivatives of uric acid. He also says, "these uric acid derivatives used in ornamentation, are apparently confined to the Pieridae alone among butterflies." Hence when a Pierid mimics an insect of another family, the pigments in the two cases are chemically quite distinct. This is well seen in the genera Leptalis (Pieridae) and Mechanitis (Danaidae).

In addition to this, Griffiths ('92) finds that the green pigment found in Papilio, Parthenos, Hesperia, Limenitis, Larentia, Ino, and Halias is a derivative of uric acid, to which he gives the name of "Lepidopteric acid" and assigns the empyrical formula C_{11} H_{10} Az_2 N_8 O_{10}.

In a paper published in 1896 in the Bulletin of the Museum of Comparative Zoölogy at Harvard College, Vol. 29, I have shown, p. 226–230, that the pigments of the scales of Lepidoptera are derived by various chemical processes from the blood, or haemolymph, of the pupa, and that the haemolymph is a proteid substance containing egg-albumen, globulin, fibrin, xanthophyll, orthophosphoric acid, iron, potassium, and sodium.

III. Development of the various Colors in the Pupal Wings.

A few researches have been carried out upon this interesting topic, but as the literature is scattered and has never been brought together, it will perhaps not be amiss to present a brief résumé of the principal facts which have been already ascertained.

(1) *Historical Account of previous Researches.* In 1889 Schäffer ('89) discussed the question of the order and time of appearance of the colors in the pupal wings of several of the Vanessas. Unfortunately he apparently did not make his obser-

vations at sufficiently close intervals of time, and was, therefore, led into some misstatements, which have been corrected by van Bemmelen ('89) and Urech ('91).

Van Bemmelen carried out an elaborate research upon the development of the various spots and colors upon the wings of Pyrameis cardui, Vanessa urticae, V. io, Pieris brassicae, and a few other forms. He discusses in detail the time and manner of appearance of all of the different spots upon the wing. Into these details we shall not follow him, but shall merely present his general conclusions regarding the development of the various colors. In Pieris brassicae it appears that during the first days of the pupal stage the wings are colorless and transparent; after a few days, however, the fore wings become opaque, and white; later the hind wing, also, goes through the same changes. The wings then remain unaltered until about two days before the butterfly issues. Then, very suddenly, the black spots and the yellow ground tone of the under sides appear. White is thus the primary color; black and yellow secondary. The first color to make its appearance in the case of Pyrameis cardui is a brown-yellow ground color, which may be observed in pupae four days old. The hind wings are at this time somewhat darker than the fore wings. The color then changes from darker brown to cinnamon-brown. The black spots appear later upon this delicate reddish brown ground color. The three fused spots which form the whitish band in the middle of the front edge of the fore wing appear during the last days of development, just before the completion of the final color-pattern.

Both van Bemmelen and Urech have shown that in Vanessa urticae the order of appearance of the various colors is the same as in Pyrameis cardui. The first color to appear in Vanessa urticae is a faint reddish tinge; this deepens and forms the ground color, and later the black spots appear upon it.

Urech ('91) has made a careful study of the development of the colors upon the pupal wings of Vanessa io. The wings are at first wholly white. Then in a restricted area of this white is noticed the appearance of a yellow, which forms the yellow of the mature wings. Almost contemporaneous with the development of the yellow comes the red, which appears in another part of the primitively white field, and gradually deepens in color until it forms the brownish red ground color of the adult wings. Still later another portion of the primitive white changes into the black of the mature wing. The under side of the mature wings of Vanessa io is mainly uniform black, and in this case also this color develops from the white at a very rapid rate, near the end of the pupal stage. This development of the black directly upon the white areas is quite remarkable in Vanessa io, and very different from that of both Vanessa urticae and Pyrameis cardui, where the black spots develop upon a field already tinged with red. Urech points out the fact, that some of the white spots seen in the mature wings of the Vanessas represent the "primitive white" of the pupal wings.

Finally, the latest paper upon the subject of the development of color in the pupa is that of Haase ('93), who has examined the pupae of a number of Papilios (*e. g.*, philenor, machaon, asterias, turnus, and podalirius), and finds that during early pupal life the wings are as transparent as glass; after a time, however, they change to an impure white, which soon becomes yellowish, and then the various colors which are destined to adorn the mature wings begin to appear.

If we are to learn much of fundamental import concerning the phylogeny of color in Lepidoptera, the researches should be carried out upon the lower moths, and not upon such highly specialized forms of Rhopalocera as the Vanessae.

In my paper on Wing scales, etc. (Mayer, '96, p. 232), I have come to the conclusion that dull ocher-yellow and drabs are, phylogenetically speaking, the oldest pigmental colors in the Lepidoptera. The more brilliant colors, such as bright yellows, reds, and pigmental greens, are derived by complex chemical processes, and are, phylogenetically speaking, of recent appearance.

I have made a study of the development of the colors and pattern in the wings of Callosamia promethea Linn. and of Danais plexippus Fab.

(2) *Development of Color in the Pupal Wings of Callosamia promethea.* The cocoons of Callosamia promethea are very abundant during the winter months, when they may be found hanging to the stems of the food plants of the larvae. The pupal wings remain perfectly transparent all through the winter, until about ten days before the time when the moth is destined to issue; they then become opaque white. An examination of the wings at this period shows that the scales are perfectly formed (Fig. 25, Plate **3**), except for the

lack of pigment, which is developed later. If one treats the scales at this stage with oil of cedar-wood or clove oil, they become practically invisible under the microscope, thus demonstrating that there is no pigment within them. Fig. 26, Plate **3**, gives the appearance presented by a scale taken from the light drab-colored margin of the mature wing. This is about the lightest area upon the wing, except the white spots; but it will be seen that this scale is much darker in appearance than the unpigmented one shown in Fig. 25. The white or unpigmented condition of the wing lasts for about four days. The wings then become uniformly tinged with an impure yellow or light drab, and very soon after this the colors begin to make their appearance. They first appear upon the lower surface of the wings. Fig. 28, Plate **3**, represents the under surface of the fore wing of a female in a very early stage of color development; in fact the upper surface shows, as yet, no trace of the colors. It will be seen that a few dark red streaks have appeared near the central portion of the wing, and it is worthy of note that these occupy the *interspaces between the nervures.* The ocellus near the apex of the wing appears faintly outlined upon its background of impure yellow.

Fig. 27, Plate **3**, represents the under side of a hind wing of a male in about the same stage as Fig. 28. Here, again, the red color occupies the *interspaces*, and indeed it is only later that the nervures become clouded over by it.

Figs. 29 and 30, Plate **3**, represent, respectively, the under and upper sides of the fore wing of a male about five hours after the first appearance of the colors. Upon the upper side (Fig. 30) we see two gray streaks near the base of the wing and a light cinnamon-brown color extending from the lower edge toward the middle of the wing. The ocellus near the apex is now quite apparent, but still faint in color. On the under surface (Fig. 29) the red markings have developed to a much greater extent than in Fig. 28. The outermost of the two white spots which occupy the center of this red area becomes the white central spot of the mature wing; the innermost one is soon obliterated owing to its becoming clouded over with red.

Figs. 37 and 36 represent respectively the upper surface of the fore wing and the lower surface of the hind wing of a female, slightly more advanced than in Fig. 30. Fig. 31 represents a male and Fig. 38 a female about twelve hours after the first appearance of the color. It is remarkable that in this stage the male and female wings are quite similar in general appearance, except that the ground color of the male is now a dusky gray, while that of the female is a cinnamon-brown.

From this time onward, however, the wings of the two sexes begin to differ more and more in appearance, for the ground color of the male becomes deep black, while that of the female remains cinnamon-brown. This change is well exhibited by Figs. 32 and 39, Plate **3**, which give the appearance of the upper surfaces of the male and female wings respectively at about twenty hours after the first appearance of the colors. Fig. 33 represents the hind wing of the same male whose fore wing is shown in Fig. 32. Figs. 34. 35, 40, and 41 give the appearance of the pupal wings just before emergence, when the colors are completely formed.

To summarize; Figs. 27, 29, 33, and 35 give successive stages in the development of color in the male; and Figs. 28, 36–41 give similar stages for the female. It becomes evident, from a comparison of these successive developmental stages, that the colors appear first upon the central portions of the wings, and that the outer and costal edges of the wings and the nervures are the last parts to acquire the mature coloration.

It is worthy of remark that the color-pattern of the mature male Callosamia promethea is quite a departure from the type of coloration which is commonly found among the Saturnidae. The *female*, however, conforms very well to the general pattern of the other species of the family. It is quite evident that the deep black coloration of the male is, phylogenetically speaking, a new acquisition, and that the coloration of the female represents the less differentiated and therefore, more primitive type.

It is interesting in connection with these facts to observe that the color-patterns of both male and female develop in almost identical ways up to the twelfth hour after the first appearance of the color; that then, however, the grayish ground color of the male wings begins to deepen into the characteristic jet black of the adult, while the light cinnamon ground color of the female merely becomes slightly darker as the wings mature.

(3) *Development of Color in the Pupal Wings of Danais plexippus.* Figs. 42–45, Plate **3**, are intended to illustrate four stages in the development of color in the pupal fore wings of Danais plexippus. The pupal stage of this species is of brief duration, last-

ing from one to two weeks only, according to the temperature to which the chrysalis is exposed. For the first few days the wings are perfectly transparent, but about five days before the butterfly issues they become pure white. An examination of the scales at this period shows that they are completely formed and merely lack pigment. In about 48 hours after this (see Fig. 42) the ground color of the wings changes to a dirty yellow. It is interesting to note that the white spots which adorn the mature wings remain pure white. Fig. 43 illustrates the next stage, where the black has begun to appear in the region beyond the cell. The nervures themselves, however, remain white. Fig. 44 shows a still later condition, where the dirty yellow ground color has deepened into rufous, and the black has deepened and increased in area and has also begun to appear along the edges of the nervures. In Fig. 45 the black has finally suffused the nervures, the base of the wing and the submedian nervure being the only parts that still remain dull yellow. It is apparent that in Danais plexippus, as in Callosamia promethea, the central areas of the wings are the first to exhibit the mature colors, and that the nervures and costal edges of the wings are the last to be suffused.

IV. The Laws which govern the Color-Patterns of Butterflies and Moths.

(1) *Historical Account of previous Researches.* The earliest paper upon this subject is by Higgins ('68). He came to the conclusion, that "the simplest type of color presents itself in the plain uniform tint exhibited when the scales are all exactly alike." He also thought it probable that "the scales growing on the membrane upon or near the veins would be distinguished from the scales growing on other parts of the membrane by a freer development of pigmentary matter, and that in this manner would arise a kind of primary or fundamental color-pattern, namely, a pale ground with darker linear markings following the course of the veins, *e. g.* Pieris crataegi." He also attempted to explain the formation of eye-spots by assuming that crescent-shaped markings migrate outwards from the sides of the nervures and meet so as to inclose a space.

It is, however, untrue that there is a freer development of pigment within the scales lying upon the nervures; in fact, the reverse is the case, as we have seen, in both Danais plexippus and Callosamia promethea. Higgins's explanation of the formation of eye-spots is also fallacious.

Darwin ('71, Vol. 2, p. 133) published four excellent figures from a drawing by Trimen, illustrating two simple ways in which *eye-spots* are actually formed, both diametrically opposed to Higgins's hypothesis. Darwin says that in the South African butterfly, Cyllo leda, "in some specimens, large spaces on the upper surface of the wings are coloured black, and include irregular white marks, and from this state a complete gradation can be traced into a tolerably perfect ocellus, and this results from the contraction of the irregular blotches of colour. In another series of specimens a gradation can be followed from excessively minute white dots, surrounded by a scarcely visible black line, into perfectly symmetrical and large ocelli" with several rings.

Scudder ('88–'89) and, afterwards, Bateson ('94) have shown that the ordinary eye-spots, such as those found in Morpho and the Satyridae, are invariably placed in the interspaces between the longitudinal veins of the wings, and also that they are often found repeated upon homologous places of both pairs of wings. Bateson says that ocelli are often seen upon both surfaces of the wing, the centers of the upper and lower ocelli coinciding. In the majority of cases, however, the upper and lower ocelli, although coincident, have quite different colors. The simpler sort of ocelli, such as those seen in the Satyridae or in Morpho, have their centers on the line of the fold-marks or creases of the wing. It sometimes happens that these creases seem to begin from the center of an ocellus. As these creases commonly run midway between two nervures, it usually results that the center of the eye-spot is exactly half way between two nervures. The large eye-spots of Parnassius apollo are an exception to this rule. In some Morphos, Satyridae, etc., in cell I^b of the hind wing there are often two creases and two eye-spots, one for each crease; but if there be only one eye-spot present, its center does not correspond with the middle of the cell, "but is exactly upon the anterior of the two creases." I have observed the same law for the white marginal spots in cell I^c in Ceratinia vallonia, C. fimbria, and Mechanitis polymnia.

In 1889 Scudder, in his work upon the Butterflies of New

England, called attention to the following facts: the transverse series of dark spots so often seen in the body of the wings of Lepidoptera are invariably placed *in the interspaces between* the longitudinal veins, never upon the veins themselves, excepting only in rare instances, where the spots occur at the extreme margin. He also pointed out that in many types of moths all differentiation in coloring has been greatly retarded, so far as the hind wings are concerned, by their almost universal concealment by day beneath the overlapping front wings. In these cases "the simplest departure from uniformity consists of a deepening of the tint next the outer margin of the wing." It is but a step from this condition to a band of dark color or a row of spots parallel with the margin. This explains why the transverse style of markings, for the hind wings at least, is so common. Scudder showed that "the number of instances, in butterflies, in which similar markings appear in the same areas of the two wings, and in the same relative position in these areas, is far too common to be a mere coincidence. It is most readily traced in the disposition of the ocelli, which are very apt to be similar in size and perfection, and to be situated between the same branches of homologous veins."

(2) *Laws of Color-Patterns.* As a result of my own study of the wings of moths and butterflies, I am prepared to propose the following additional laws of color-patterns. (*a*) Any spot found upon the wings of a moth or butterfly *tends to be bilaterally symmetrical both as regards form and color*, the axis of symmetry being a line passing through the center of the interspace in which the spot is found, and parallel to the direction of the longitudinal nervures. For example, in Figs. 6 and 7, Plate **2**, each spot is bilaterally symmetrical about the axis HH. The same law holds for the spots represented in Figs. 8–14 and 16.

(*b*) Spots tend to appear *not in one interspace only*, but as a row occupying homologous places in successive interspaces. Indeed we almost always find similar spots arranged in linear series, each similar in shape and color to the others and occupying the center of its interspace. The rows of spots represented in Figs. 8–14 and 16 will suffice to illustrate this law.

It is interesting to notice that bands of color are often made by the fusion of a row of adjacent spots; and, conversely, chains of spots are often formed by the breaking up of bands, leaving a row of spots occupying the interspaces. Many instances of this are to be seen in certain specimens of various species of the Heliconidae. For example, in Heliconius eucrate (Fig. 58, Plate **4**) I have observed that certain specimens show a row of distinct spots in place of the, usually entire, band which crosses the middle of the hind wing. In fact, the vast majority of bands can be analyzed into a series of similar elements, each element occupying an interspace. Thus, in Plate **2**, Fig. 17, which represents a wing of Saturnia spini, the band seen crossing the wing parallel with its margin is made up of a series of fused crescents, each crescent occupying an interspace.

If, on the other hand, this band were to break away from the nervures, the result would be a series of crescent-shaped spots each occupying the center of an interspace. It is very interesting to observe the manner in which bands degenerate and disappear. Numerous opportunities for doing this may be had among the Heliconidae. In some species, as in Melinaea parallelis, hardly any two specimens are alike in the condition of the black band across the middle of the hind wings. *The most common method of disappearance is a shrinking away of the band at one end.* This is well illustrated in Figs. 84–87, Plate **7**, which represent a sort of "Mercator's Projection" of the wings of Mechanitis isthmia (for explanation of the plan of projection see page 207.) Fig. 84 represents a male, showing a well-marked band of hardly separated spots extending across the middle of the hind wing. Fig. 87 shows a female in which the spots are thinner and more crescentic and the separations much more marked. Fig. 85 is also drawn from a female, in which it will be seen that the band has shrunk away leaving only a portion of it at the right, and in Fig. 86, which represents another female specimen, only one faint spot is left.

It is very common to find bands shrinking away at *one* end. Sometimes, however, they shrink away at *both* ends, and very often they break up into a row of spots, which may then contract into the centers of their interspaces and finally disappear. It is worthy of note that it is *very* rare to find a band breaking at the middle of its length and each half receding from the other. Such a case is, however, shown by Melinaea parallelis (see Fig. 82, Plate **7**), where one sometimes finds specimens in which the black band across the middle of the hind wings is complete and unbroken; whereas in other specimens, as in Fig. 82, it is partially broken in the middle, and in still others the break has become a wide gap by the drawing away of the halves of the band from each other.

We see, then, that it is very common to find bands shrinking away from either end, but very rare to find them broken in the middle region. This, however, is only a special case of the law enunciated by Bateson ('94), that the ends of a linera series are more variable than the middle. Almost any row of spots also exhibits the same law, in that the spots occupying the middle portions of the row are similar one to another, while those at the ends of the series depart more or less from the type. (See Figs. 10–13, Plate **2**.)

The position of spots which are situated near the edge of the wing is largely controlled by the wing-folds or creases. In Melinaea egina (Fig. 96, Plate **8**) there is a row of white spots near the outer edges of the wings, and each of these spots is cut in two by a narrow black line which extends along the wing-fold. Also in Ceratinia vallonia (Fig. 81, Plate **7**) and in many other forms of the Danaoid Heliconidae one often finds two creases in a cell, and in this case there are two marginal spots, one on each crease. In many other cases, however, the marginal spots are double in each cell, although there is but a single wing-fold; the spots in these cases are situated at some distance on either side of the fold. (See Figs. 95, 96, Plate **8**.) Another very common condition is exemplified in Fig. 83, Plate **7**, where there is a single marginal spot situated upon the wing-fold in each cell.

(3) *Detailed Discussion of the Laws of Color-Patterns.* Figs. 6–14 and 16, Plate **2**, are taken from special cases which serve to illustrate the two chief laws of color-pattern, *i. e.*, that spots tend to be bilaterally symmetrical about an axis (HH, Figs. 6, 7) passing through the center of the cell parallel with the nervures; and also, that spots of similar shape and color tend to be repeated in a row of adjacent cells.

In Fig. 7 the spots are separated in the middle, but still incline outward symmetrically from the center; indeed, instances of double spots are very common. In such cases, however, each half spot is a reflection of its mate on the other side of the axis passing through the center of the cell.

Fig. 8 represents various eye-spots found in the Morphos, and will serve to illustrate the laws of eye-spots which have been enunciated by Scudder ('89) and Bateson ('94). These spots occupy the center of the cells in which they are found. In cell II, for example, is a large eye-spot with a crescent in its center, and it will be observed that this crescent follows the general law and is bilaterally symmetrical about the usual axis.[1]

Fig. 9 shows the law of repetition of some very complex spots, each being bilaterally symmetrical. It is found in Parthenos gambrisius.

Figs. 10 and 11 represent Ornithoptera urvilliana and O. priamus respectively. In Fig. 10 we see an instance of a spot within a spot, and in Fig. 11 an even more complex case, for here there are three systems of spots one within another.

Fig. 12 represents the marginal markings found in Hestia jasonia and Fig. 13 Hestia leuconoe var. clara. These two examples are intended to illustrate the fact, that, although the markings are situated *upon* the nervures, they are bilaterally symmetrical not *about the nervures* as axes, but about the usual axis passing midway between the nervures. In Fig. 12 it will be seen that the two curved markings situated upon nervures 1^b and 2, and projecting into cell I^c, are bilaterally symmetrical only in reference to the axis through the middle of the cell.

In allied species the spot situated upon nervure 1^b is often absent. The system of markings is therefore undergoing degeneration at this end (cf. Fig. 13, cell I^c). The curved mark upon nervure 5 (Fig. 12) projecting into cell V is plainly symmetrical with respect to its fellow in the opposite side of cell V, and not with its near companion which projects into cell IV. The same is also true in the case of the spots in cell VI.

In Fig. 13 the spots appear at the first glance to be bilaterally symmetrical about both nervures and centers of cells, but in cell IV the marking situated on nervure 4 does not quite reach to the center, and it is interesting to observe that its fellow on nervure 5 also falls short of reaching the center and is therefore symmetrical with respect to the other curved spot in cell IV. This case also furnishes an instance of a break in the middle of a linear series.

Fig. 14 is taken from the under surface of the hind wing of Papilio emalthion. It serves to illustrate the fusion of two originally separate rows of spots. In this case the crescent-shaped spots above have fused with the rectangular ones below, so as to inclose a portion of the ground color of the wing. Sometimes two rows of spots of different colors fuse, giving a chain of spots which are of one color above and another below.

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[1] A very beautiful exception (Fig. 19, Plate 2) to this rule for the crescents found in eye-spots is seen in the under surface of the fore wing of Missanga patinia Moore. It will be noticed that the large black crescent found in this beautiful eye-spot is 90° away from its usual position. This is the only exception of the sort known to me.

In Fig. 16 the spots composing the row BB are blue (dark) above, and red (light) below. It will be observed that the color is bilaterally symmetrical, as usual, about the axis through the middle of the cell. Such bicolored spots are often due to a simple fusion, as before stated; but sometimes they may, perhaps, be intrinsically bicolored.

Fig. 15 is a beautiful instance of an exception to the general rule that spots are bilateral about the axis through the center of the cell. It is taken from Ornithoptera trojana Staudinger.[1] The light spots represented near the outer edge of the wing are of a brilliant iridescent green. It is evident that they are distinctly bilateral with respect to the *nervures*; especially is this true of the pair adjacent to nervure 1. Ornithoptera brookiana Wallace illustrates another exception, though in a less marked degree.[2] Other allied species of Ornithoptera, however, would seem to show that these apparent exceptions may have been derived from forms which exhibited two spots in each cell and followed the usual rule. These are the only instances of such exceptions known to me. I do not doubt, however, that further study would reveal others.

In Fig. 17 an example is given of the peculiar kind of eye-spots found in the Saturnidae. The species from which the figure was taken is Saturnia spini. It will be seen that this so-called eye-spot is quite different in formation from the ocelli of butterflies. It is simply a series of curved cross-bands between nervures, arranged symmetrically on both sides of the cross vein CC. The "eye-spots" upon the wings of Attacus luna and in the genus Telea are also of this sort. True eye-spots, however, similar to those found among the Morphos and Satyridae, occur in moths, as in the apex of the fore wing of Samia cecropia, Callosamia promethea, etc. "False" eye-spots are also found on the wings of butterflies; in Vanessa io, for example, the so-called eye-spot of the fore wing has been shown by Dixey ('90) to be made up of a series of fused spots. It will be remembered that Merrifield ('94, Plate 9, Fig. 4) caused this "ocellus" to break up into its constituents by subjecting the pupa to a temperature of 1° C. The ocellus upon the hind wing of Vanessa io is no doubt a true eye-spot; the only evidence which might lead one to infer that the ocellus of the fore wing was of the same character is, that an aberrant form is sometimes found in nature having the "eye-spots" on both fore and hind wings obliterated, thus indicating a *possible* connection between the two (see South, '89).

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[1] See Watkins, '91, Plate 4.

[2] See Hewitson, '56-'76, Vol. 1.

Fig. 18 is intended to illustrate the process of degeneration occurring in bands. Band BB is represented as breaking down by the rare method of parting in the middle. Example, Melinaea parallelis. Band EE is degenerating at one end; this is a very common method.

Figs. 20–23 represent hypothetical conditions not found in nature; all being contrary to the conditions of the laws which have just been stated.

In Fig. 20 row RR presents three spots for each cell. I believe this has not been found in nature, but I should not be surprised if it were discovered, for it is not contrary to any of the laws.

Row CC, on the other hand, is contrary to the law of bilaterality, the crescents not being bilateral about axes passing through the middle of the interspaces parallel with the longitudinal nervures.

Fig. 21 is intended to show a series of spots arranged side by side in twos in each cell, and of different colors. This, I believe, is impossible, for it is contrary to the law of bilaterality of color arrangement about the usual axis (HH, Figs. 6, 7).

In Fig. 22 there are several conditions which are impossible; *e. g.*, an eye-spot situated upon a nervure is never seen in nature, also two spots originally side by side, as in cell III, *never rotate* around each other so as to come to lie one above the other. Spots often move, however, as shown by the arrows in cell IV, thus giving rise to fusions; or they may move away from each other, causing a wider gap between the rows. In cell I^b are shown two looped spots. One form (A) is quite usual, being found indeed in Cymothoe caenis Drury.[1] The other form of spot (D) is an impossibility, not being bilaterally symmetrical.

Fig. 23 illustrates other impossibilities in color-pattern, none of them, of course, being found in nature. For example, one never finds a row of slanting spots such as SS. Also one never sees a row of similar spots in *alternate* interspaces, such as is shown in DD, for this would be contrary to the law that similar spots are repeated in a row of adjacent interspaces. These last four diagrams

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[1] See Cramer (1779–'82), Vol. 2, Plate 146.

(Figs. 20–23) have been introduced merely to give an idea of the curiously strict limitations which nature has imposed upon the differentiation of the color-pattern. Many beautiful effects might have been produced, such for example as that of alternate interspaces showing different colors, but this is not seen in nature.

It is interesting to recall the fact, that the colors themselves are impure and by no means so brilliant as they, perhaps, might have been, had Natural Selection been more severe in regard to color.

There is doubtless some physiological reason why spots almost invariably appear and disappear in the *middle of the interspaces*, and when we know more of the anatomical and histological conditions of the wing during the development of the colors, we may be able to discover it. It will be remembered that in the developing pupal wings of Callosamia promethea and Danais plexippus I found that the colors first made their appearance in the interspaces, and finally spread out so as to tinge over the nervures.

(4) *Origin of Color-Variations.* There is every reason to believe that all kinds of spots and bands, which are essentially only fused spots, may appear or disappear in any individual specimen without going through a long course of Natural Selection and slow phylogenetic differentiation. Darwin and Trimen ('71) and Bateson ('94) have demonstrated that this is true for eye-spots. In the Heliconidae I have found that bands and rows of spots are very variable in different specimens of the same species (see Plate **7**, Figs. 84–87).

There is a large and widely scattered literature recording the appearance and disappearance of colors and markings upon the wings of Lepidoptera. Limits of time and space prohibit my doing justice to it here, but it may be well to call attention to a very few of the more recent papers upon the subject. Many of the color-aberrations recorded in this list of papers may be due to the direct influence of environmental conditions upon the individual, but others are no doubt true sports or, to speak crudely, "congenital" variations, and might under favorable conditions of life become the ancestors of *new* varieties or species. It seems highly probable that new species often arise from just such sports in the manner so frequently and ably expounded by Bateson.

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(5) *Climate and Melanism.* Lord Walsingham ('85), in his presidential address before the Yorkshire Naturalists' Union, brought forward the idea, that, although Arctic insects might be perfectly

able to withstand the most severe cold while in hibernation during the winter, it is of great importance for them to absorb as much heat as possible during the short summer. He placed several species of lepidopterous larvae upon a snow surface exposed to bright sunshine. The snow melted at different rates under the various larvae, and in two hours the darkest insect had sunk by far the deepest into the snow, proving that it was the best absorber of heat. This ingenious experiment of Lord Walsingham should be made the beginning of an extensive and careful research.

Chapman ('88) has shown that it may be of advantage to moths inhabiting wet regions to display dark colors, or become melanic. His observations were made upon Diamea flagella, and he says that upon one showery afternoon he observed that one side of the tree trunks was wet and dark in color; the other side being dry was paler. "As a consequence, the dark specimens of flagella were very conspicuous upon the dry portions, hardly visible on the wet, whilst with the ordinary form the conditions were reversed, those on the wet bark were conspicuous, those on the dry much less so." Perhaps the dull coloration of Arctic moths may be partially due to the effect of the somber background of rocks in the regions which they inhabit.

(6) *Relation between Climate and Colors of Papilios.* It is well known that the Lepidoptera in the Tropics display the richest variety and greatest number of colors. I have counted the colors exhibited by the 22 species of Papilio enumerated by Edwards as inhabiting North America north of Mexico, and also those which are displayed by the 200 species of Papilio named in Schatz's list as found in South America. The "colors" were determined by comparison with the colored plates in Ridgway ('86).

In this manner it was determined that the North American Papilios exhibit 17 colors, viz., black, brown, primrose-yellow, canary-yellow, sulphur-yellow, orange, white, greenish white, apple-green, cream-color, azure-blue, sage-green, rufous, pearl-gray, indigo-blue, iridescent blue, iridescent green.

On the other hand the South American Papilios exhibited 36 colors, viz., black, translucent black, brown, white, canary-yellow, citron-yellow, olive-yellow, primrose-yellow, chrome-yellow, straw-yellow, gamboge-yellow, cream-color, greenish white, apple-green, malachite-green, emerald-green, sage-green, slaty green iridescence, pea-green, azure-blue, iridescent Berlin-blue, indigo, pearl-blue, glaucous blue, salmon-buff, écru-drab, flesh-color, coral-red, rose-red, vermilion, rufous, geranium-red, geranium-pink, olive-buff, iridescent geranium-pink (as in P. zeuxis), and transparent areas.

As 200 species in South America display but 36 colors, while 22 in North America show 17, it follows that, while the number of species in South America is 9 times as great as in North America, the number of colors displayed is only a little more than twice as great. The richer display of colors in the Tropics, therefore, *may* be due simply to the far greater number of species, which gives a better opportunity for color-sports to arise, and not to any direct influence of the climate. The number of broods, also, which occur in a year is much greater in the Tropics than in the Temperate Zones, so that the Tropical species must possess a correspondingly greater opportunity to vary.

V. THE CAUSES WHICH HAVE LED TO THE DEVELOPMENT AND PRESERVATION OF THE SCALES OF THE LEPIDOPTERA.

(1) *Experiments and Theory.* It is well known that the scales of Lepidoptera are morphologically identical with hairs. Indeed, a graded series from simple hairs, such as are found covering the body-surface of most Arthropods, up to perfectly developed flat scales bearing well differentiated striae may usually be found upon one and the same insect.

It is also remarkable that the color-bearing scales of beetles have been developed in the same manner as those of moths and butterflies, and that in this case also hairs have become differentiated into scales which are precisely similar in appearance to those of the Lepidoptera (see Dimmock, '83).

This is only another of the numerous instances met with in nature where similar conditions of selection have developed complex organs which are similar in appearance, though found in widely separated groups. A list of papers relating to the development of scales has been given by Dimmock ('83, p. 1–11).

Most of the hairs which cover the body-surface in Arthropods are true sensory structures, the axis of each of which is a protoplasmic process from a single cell of the hypodermis, which lies below the cuticula. They have probably been developed because the cuticula, being hard, chitinous, and inflexible, would serve but poorly as a tactile or sensory surface.

Of course no one would venture to ascribe any sensory function to the scales which cover the wing-membranes of the Lepidoptera. We may, however, make several more or less reasonable hypotheses concerning the probable uses of the scales, and by testing these suppositions arrive perhaps at some plausible explanation of their retention and the complex development which they have undergone.

(1) They may have caused the wings of the ancestors of the Lepidoptera to become more perfect as organs of flight, by causing the frictional resistance between the air and the wing-surface to become more nearly an optimum.

(2) The appearance and development of the scales may have served, as Kellogg ('94) has suggested, "to protect and to strengthen the wing-membranes."

(3) The present development of the scales may be due to the fact that they displayed colors which were in various ways advantageous to the insects.

Concerning the first of these three hypotheses, the wing has, broadly speaking, two chief functions to perform in flight. It must beat more or less downward against the air, and must, in addition, glide or cut through the air, supporting the insect in its flight. For the mere beating against the air a relatively *large* co-efficient of friction between the air and the wing might be advantageous; but for gliding and cutting through the air a *small* co-efficient of friction would certainly be an advantage. There must therefore be an optimum co-efficient of friction, which lies somewhere between these two.

In order to determine the co-efficient of friction between the wing and the air, use was made of a method which, in one form or another, has long been known to engineers; that is, of observing the ratio of damping of the vibrations of a pendulum.

It is well known that when a pendulum is swinging free, and uninfluenced by any frictional resistances, the law of its motion is expressed by the formula,

$$(1)\quad d = A \sin \frac{2\pi}{T} t$$

where d is the displacement of the pendulum from its middle position after the interval of time t, A is the maximum displacement and T the time of a complete vibration, back and forth. If, however, frictional resistances interfere, the formula becomes,

$$(2) \quad d = A\, e^{-Kt} \sin \frac{2\pi}{T_1} t \qquad ,$$

$$(3) \quad \text{Hence, } K = \frac{-\log d\ T_1}{A \log e \sin 2\pi\ t^2}, \text{ or if } t = T_1$$

$$(4) \quad K = \frac{-\log d}{AT_1 \log e}$$

where K is a constant dependent upon the friction, e is the base of the Napierian system of logarithms and T_1 is the time of a complete vibration, which may be different from the T, representing the time of vibration when not under the influence of friction.

The plan was, then, to attach the wing of some large butterfly or moth to the end of a short, light pendulum in such a way that it would either fan against the air, or cut through it, and then to observe the ratio of damping of the pendulum's vibrations. A drawing of the pendulum with a wing attached is given in Plate **1**, Fig. 3. The wing is here shown in the position for "cutting or gliding" through the air. It would be in the position for fanning against the air, if it were rotated 90°. The pendulum was made of brass and steel, the ends being of brass and the slender middle portion of steel. Its vibrations were read off upon an arc graduated in millimeters. The readings were certainly accurate down to 0.5 mm. The pendulum was hung upon a steel knife edge (x, x, Fig. 3), which rested upon firm level glass bearings. The pendulum was 24.21 cm. long, and weighed 19.61 grams. Its time of vibration (T_1) was 0.877 seconds. This rate of vibration was practically unaltered when a wing was fastened to the end of the pendulum, the reason being that the wings were very light, the heaviest, that of Samia cecropia, weighing only 0.038 grams. The wing to be experimented upon was fitted into a deep, narrow slot at the free end of the pendulum, and then cemented in by means of a little melted beeswax. It thus became a perfectly rigid part of the pendulum itself.

The pendulum with wing attached was deflected through a known arc, read off upon the millimeter scale, and its reading at the end of the first swing carefully observed. Then if A be the initial deflection, which we may call unity, and if d be the reading after the first swing, the ratio of damping is given by the expression $\frac{d}{A}$. In experimenting with a fore wing of Samia cecropia "fanning the air," it was found, as the mean of many trials, that this ratio of damping was 0.919, that is to say, the amplitude of the 2d swing was 0.919 as great as the amplitude of the 1st, that of the 3d only 0.919 as great as that of the 2d, and so on. The scales were then carefully removed from the wing-membranes, by means of a camel's hair brush, and by again testing the vibrations it was found that the new ratio of damping was 0.917. This is so near the value of the ratio of damping with the scales on (0.919), that it may be considered identical, the difference being due to errors of experimentation.

Hence we must conclude that the presence of the scales upon the wing-membrane has not altered, appreciably, the co-efficient of friction which would exist between scaleless wing-membranes and the air. The results indicate rather, that when the scales appeared upon the wings of the scaleless, clear-winged ancestors of the Lepidoptera, the co-efficient of friction remained unaltered. This tempts one to the further conclusions, that the co-efficient of friction between the air and the wings was already an optimum in these clear-winged ancestors before the appearance of the scales, and therefore that Natural Selection would operate to keep it unaltered.

A wing of Samia cecropia cut so as to give it the same shape and dimensions as one of Morpho menelaus, gave an identical damping ratio. I conclude that the co-efficient of friction may be the same for both moths and butterflies, at least for those which move their wings at about the same rate in flight.

It was found in the case of the Samia cecropia wing, that when it was vibrated in the position for "cutting through" the air, the ratio of damping was 0.991. It will be remembered that, when the wing "fanned" the air, this ratio was 0.917. We may find the ratio between the resistance encountered in "fanning" and that encountered in "gliding" through the air by substituting these values in equation (*4*), $K = \frac{-\log d}{AT_1 \log e}$.

Thus for fanning, $\frac{d}{A} = 0.917$ and $T_1 = 0.877$. Making A unity.

$$K = \frac{-\log 0.917}{0.877 \log e} = 0.1.$$

In cutting through the air, $\frac{d}{A} = 0.991$ and T_1 as before $= 0.877$.

Hence in this case $K = \frac{-\log 0.991}{0.877 \log e} = 0.01.$

The wing, then, encounters at least 10 times the resistance in fanning that it does in gliding through the air. It should be said that this last experiment is somewhat crude, for the wing necessarily could not be made to cut the air with that delicate precision which is probably realized by the insect in flight. I should not be surprised, if in nature the insects encountered at least 20 times the resistance in beating the air, that they do in merely gliding through it.

Concerning Mr. Kellogg's supposition, that the scales were developed to "protect and to strengthen the wing-membranes," I will admit that they may serve in some slight degree to protect the wing-membranes from scratches, etc.; but I am unable to accept his conclusion, that they strengthen the wing-membranes, any more than that the shingles upon a roof serve to add strength to it. The wing-membranes themselves are tough, elastic, and not easily torn or scratched, and the scaleless wings of the Neuroptera and Hymenoptera are very rarely found torn or scratched in nature.

In 1858 Mr. Alexander Agassiz called attention ('59) to the fact, that "the nervures of the wings of butterflies are so arranged as to give the greatest lightness and strength; they are hollow, with their greatest diameter at the base of the wing, the point of greatest strain, their diameter gradually diminishing to the edge of the membrane. If a section be made across such a wing parallel to the axis of the body, we find very much the arrangement which has been experimentally proved by Fairbain and Stephenson as giving the greatest strength of beams, as exemplified in the tubular bridge. We find the strongest nervure placed either on or near the anterior edge of the upper wing; there is no such nervure on the lower wing, all being of nearly the same size, as such a one would have prevented the elasticity of the wing from assisting the flight to any considerable extent." Mr. Agassiz has informed me that he carried out an extensive series of experiments upon the rigidity of the wings of various species of Lepidoptera. He placed little platinum strips upon the wings and observed the extent of the bending produced. His results demonstrated that the Sphinx moths possess by far the strongest wings, and that the Danaoid and Acraeoid Heliconidae have very weak wings. The reason for this probably lies in the fact, that the Sphinx moths move their wings with great rapidity, while, according to Bates ('62) and all subsequent observers, the Heliconidae have a slow flight.

As the scales have been developed not because they aided the insects in flight or strengthened the wings, their retention must have been due to some other cause, probably to their displaying colors which were advantageous to their possessors in various ways. As Dimmock ('83) says, "it is only in insects where certain kinds of brilliant coloration have been developed that one finds scales." Indeed, I believe that the vast majority of the scales found in Lepidoptera are merely color-bearing organs. They probably first made their appearance upon small areas of the wings, perhaps adjacent to the body, and were merely colored hairs, similar to those of the surface of the body, which had grown out upon the wings. In this position they displayed some color which was of advantage to the insect; perhaps serving to render it less conspicuous than formerly. Under these circumstances they would naturally be preserved through the operation of selection until finally they became modified into true scales; just as the hairs in the Coleoptera have undergone a similar modification. If this be true, it is easy to see how they might spread out over the surfaces of the wings until the whole wing became covered with scales.

(2) *Summary of Conclusions.* The scales do not aid the insects in flight, for the wings have precisely the same efficiency as organs of flight when the scales are removed. The phylogenetic appearance and development of the scales upon the scaleless ancestors of the Lepidoptera did not in the least alter the efficiency of their wings as organs of flight. This efficiency of their wing surfaces was probably, therefore, already an optimum before the scales appeared. The scales do not appreciably strengthen the wing-membranes, that function being performed by the nervures. The majority of the scales are merely color-bearing organs, which have been developed under the influence of Natural Selection.

PART B.

COLOR-VARIATIONS IN THE HELICONIDAE.

I. General Causes which determine Coloration in the Heliconidae.

In 1861, after eleven years of study within the forests of South America, Bates read his, now classic, paper upon the life and habits of the Heliconidae of the Amazon region. In it he first brought forward his ingenious theory of Mimicry—a theory which, under the able interpretations of Wallace and Fritz Müller, and in more recent times, under the impetus of the zeal of their numerous disciples, has yielded so much that is of interest to scientific men.

The Heliconidae are, above all, creatures of the forest, and Bates found that the number of species increases as one travels inland from the Lower Amazons towards the eastern slopes of the Andes, so that the hot Andean valleys near Bogota, or in Ecuador, contain perhaps the greatest number. In their range they are restricted to the Tropics of the New World. Only two species, Dircenna klugii and Heliconius charitonius, extend so far north as the extreme Southern States of the United States, and none of them are found much further south than 30° S. Lat.

Bates and Felder first saw that the Heliconidae were naturally divided into two distinct groups. One, the Danaoid Heliconidae, consists of about twenty genera, all more or less closely related, and evidently an offshoot from the great universal family, the Danaidae, members of which are found in both Hemispheres. The other group, the true Heliconidae, is composed of two closely related genera, Heliconius and Eueides. They are allied in structure to the Acraeidae and hence their name, Acraeoid Heliconidae. Schatz and Röber ('85–'92, p. 105) say of the Acraeoid Heliconidae: — They are an offshoot of the great family Nymphalidae, which have undergone a remarkable development in the length of the fore wing, and in this respect have been developed in a direction parallel with the Danaoid Heliconidae. In their structure, however, they are quite distinct from the Danaoid group.

Schatz has proposed a new classification for the Heliconidae. He finds that the genera Lycorea and Ituna, which Bates included among the Danaoid Heliconidae, are very closely allied to the Danaidae, he therefore says that Lycorea should be placed among the Danaidae, while Ituna is clearly midway between the Danaidae and the Danaoid Heliconidae. Schatz proposes the name "Neotropidae" for the Danaoid Heliconidae. However, I think the name "Danaoid Heliconidae," being older and more descriptive of their relationship, should by all means be retained. In this paper I shall follow Bates's classification, and include among the Danaoid Heliconidae the twenty genera: Lycorea, Ituna, Athesis, Thyridia, Athyrtis, Olyras, Eutresis, Aprotopos, Dircenna, Callithomia, Epithomia, Ceratinia, Sais, Scada, Mechanitis, Napeogenes, Ithomia, Aeria, Melinaea, and Tithorea. The Acraeoid Heliconidae will then consist of the two remaining genera, Heliconius and Eueides.

Staudinger ('84-'88) records 453 species belonging to the Danaoid group, and 150 belonging to the Acraeoid group.

Nearly all that we know concerning the early stages of the Heliconidae is due to Wilhelm Müller ('86). He gives figures and more or less complete descriptions of the early stages of Dircenna xantho, Ceratinia eupompe, Ithomia neglecta, Thyridia themisto, Mechanitis lysimnia, and also of Heliconius apseudes, H. eucrate, H. doris, Eueides isabella, E. aliphera, and E. pavana. Bates ('62, p. 596) says that he raised the larvae of Heliconius erato and Eueides lybia. Schatz and Röber ('85-'92) figure the larva and pupa of Ceratinia euryanassa. Edwards has given a detailed account of the early stages of H. charitonius.

Müller found that the larvae of the Danaoid group feed on various species of Solanum, while the genera Heliconius and Eueides feed upon the Passifloreae. The larvae are conspicuously colored, and often gregarious; they seem to take but little pains to hide themselves during the chrysalis stage, for Müller says that he has seen the silver-spotted, white chrysalids of Heliconius doris hanging in great numbers in the near neighborhood of the larval food plant. The mature insects also furnish a good example of what Wallace ('67) designated as "warning coloration," for their tawny orange and black wings are very conspicuous as they sail slowly around in circles, settling at frequent intervals in their lazy irregular flight.

Bates was the first to call attention to the circumstance that they often possess a rather strong and disagreeable odor, and in 1878 Fritz Müller confirmed this observation for a number of the Heliconidae. He found, for example, that the genera Ituna and Ilione have a pair of finger-like processes near the end of the abdomen, which can be protruded and then emit a rather disagreeable odor; and he also found that the Acraeoid Heliconidae, especially the females, possess a disgusting odor. Seitz ('89), however, examined about fifty species of Heliconidae and found that many of them appear to have no odor. For example, he says that Heliconius eucrate and Eueide dianasa have no odor, but that *some specimens* of Heliconius beskei, and Eueides aliphera have a horrid odor.

Whether they are odorous or not, it would seem that the Heliconidae have but few enemies to fear, for not one of the many skilled observers who have studied them in their native haunts has ever seen a bird attack them. and the only ground for believing that they are attacked rests upon the rather dubious evidence of a few specimens found by Fritz Müller having symmetrical pieces apparently bitten out of the hind wings. Belt ('74) observed that a pair of birds which were bringing large numbers of dragon-flies and butterflies to their young never brought any of the Heliconidae, although these were abundant in the neighborhood. In fact, Belt was able to discover only one enemy of these butterflies, and that was a yellow and black wasp, which caught them and stored them up in its nest to feed its young. The Heliconidae then, in spite of their weak structure, conspicuous colors, and slow flight, enjoy a peculiar immunity.

As is well known, Bates ('62) first called attention to the fact that the Heliconidae were "mimicked" or imitated both in color-pattern and shape of wings by a number of other genera of butterflies and even moths. Bates had no difficulty in showing that this mimicry might easily be explained upon the ground that the Heliconidae, on account of their bad taste and smell. were immune from the attacks of birds and other insectivorous animals, and that therefore it gave a peculiar advantage to a butterfly belonging to any other group not thus protected, to assume the shape and coloration of the Heliconidae; for then the birds could not perceive any difference between it and the true Heliconidae. Bates found that fifteen species of Pieridae belonging to the genera Leptalis and Euterpe, four Papilios, seven Erycinidae, and among diurnal moths three Castnias and fourteen Bombycidae imitate each some distinct species of the Heliconidae occupying the same district. He also found that all of these insects were much rarer than the Heliconidae which they imitated. In some cases, indeed, he estimated the proportion to be less than one to a thousand. Wallace ('89, p. 265), who has added so much to our knowledge of this subject, aptly defines this kind of mimicry as an "exceptional form of protective resemblance."

But by far the most remarkable discovery made by Bates was the fact, that species belonging to different genera of the Heliconidae themselves mimic one another. Neither Bates nor Wallace was able to give any satisfactory explanation of the cause of this latter form of mimicry, for all of the genera of the Heliconidae are immune. They therefore supposed it to be due to "unknown local causes," or similarity of environment and conditions of life.

Thus the matter rested until 1879, when Fritz Müller brought out his well-known paper upon "Ituna and Thyridia, a remarkable example of mimicry," in which he showed that both of these genera are protected, yet they mimic each other. He also showed that this mimicry might be due to Natural Selection brought about in the following manner. It is possible that young birds, upon leaving the nest, are not furnished with an unalterable instinct which tells them exactly what they should and should not eat; so they may try experiments, and would then in all probability taste a few of the Heliconidae before finding out that they were unfit to eat. Müller then demonstrated that, if this supposition be true, it becomes a decided advantage to the various species of Heliconidae to resemble one another. His reasoning was as follows: Let it be supposed that the young and inexperienced birds of a region must destroy 1,200 specimens of any distasteful species of butterfly before it becomes recognized as such, and let us assume further that there are in existence 2,000 specimens of species A, and 10,000 of species B; then, if these species are *different* in appearance, each will lose 1,200 individuals, but if they resemble each other so closely that they cannot be distinguished apart, the loss will be divided pro rata between them, and A will lose 200, and B 1,000; therefore A saves 1,000 or 50% and B saves only 200 or 2% of the total number of individuals in the species; hence, while the relative numbers of the two species are as 1 to 5, the relative advantage derived from the resemblance is as 25 to 1.

Blackiston and Alexander ('84) have given a complete mathematical statement of Müller's law, and have come to the conclusion that, if the number of individuals destroyed is small compared with the number constituting the species, the relative advantage is inversely as the square of the original numbers; but if the number destroyed is large compared with the original number, the ratio of advantage is much greater than the inverse squares of the original numbers. Their deduction may be briefly stated as follows:—

Designation of Species	A	B
(1) Original number	$a >$	b
(2) Number lost without imitation . .	e —	$= e$
(3) Remainders without imitation . .	$(a-e)$	$(b-e)$
(4) Number lost with imitation . . .	$\frac{a}{a+b}\,e$	$\frac{b}{a+b}\,e$
(5) Remainders with imitation	$a\left(1-\frac{e}{a+b}\right)$	$b\left(1-\frac{e}{a+b}\right)$
(6) Excess of remainders due to imitation, or "absolute advantage" (3)—(5) . . .	$\frac{b\,e}{a+b}$	$\frac{a\,e}{a+b}$
(7) Ratio of excess to remainders without imitation (6): (3), =proportional advantage.	$\frac{e}{a+b}\times\frac{b}{a-e}$	$\frac{e}{a+b}\times\frac{a}{b-e}$
(8) Ratio of proportional advantage of B to proportional advantage of A.	$=\frac{a\,(a-e)}{b\,(b-e)}=\frac{a^2}{b^2}\,\frac{\left(1-\frac{e}{a}\right)}{\left(1-\frac{e}{b}\right)}$	

It is evident, then, if e be small compared with a and b, that the proportional advantage of B is to the proportional advantage of A as a^2 is to b^2. If, however, the loss (e) is great compared with a or b, the relative gain for the weaker species becomes even greater than the ratio of the squares of b and a.

If it be true, then, that young birds, when they leave the nest, do *not* possess a directing instinct telling them what they should and should not eat, but actually do experiment to some extent upon various insects which they meet with, Müller's law is amply sufficient to account for the numerous cases of mimicry and remarkably close resemblances which are found among the species of the Heliconidae themselves.

Unfortunately no *direct* experiments have ever been made upon the feeding-habits of young South American birds, nor have the contents of their stomachs been examined. There have been a few experiments, however, which seem to support the idea that some animals do learn to associate an agreeable or disagreeable taste with the coloration and appearance of their prey. It is well known that Weismann ('82, p. 336–339) found that the black and yellow larvae of Euchelia jacobaeae were refused by the green lizard of Europe. He then introduced some young caterpillars of Lasiocampa rubi, which are very similar in appearance to those of Euchelia. The lizards first cautiously examined the larvae, and finally ate them. After this Weismann reintroduced the E. jacobaeae larvae and the lizards were seen to taste them, apparently mistaking them for the edible L. rubi caterpillars.

Poulton ('87) carried out a most careful and well-conducted research upon the protective value of color and markings in insects in reference to their vertebrate enemies. He experimented upon three species of lizards and a tree-frog. Poulton combines his results with those of other observers and presents them in the form of a table, which certainly supports the suggestion of Wallace ('67), that brilliant and conspicuous larvae would be refused as food by some at least of their enemies. Poulton also shows that a limit to the success of this method of defence (conspicuous larvae having unpleasant taste or smell) would result from the hunger which the success itself tends to produce. In the Tropics, indeed, where insectivorous birds and lizards are far more numerous than with us, and where competition for food is great among them, "we may feel sure that some at least would be sufficiently enterprising to make the best of unpleasant food, which has at least the advantage of being easily seen and caught." This last suggestion of Poulton certainly seems reasonable; moreover, it has occurred to me that young birds, being but little skilled in the art of obtaining their food, might quite often be forced by hunger to try various kinds of insects, and perhaps even the Heliconidae themselves.

Beddard ('92, p. 153–167) reports the results of an extensive series of experiments carried out by Mr. Finn and himself upon marmosets, birds, lizards, and toads. He arrives at conclusions which are quite different from those of Poulton and others, but it appears to me that his experiments were by no means so critically performed as those of Poulton. He frequently threw larvae into a cage containing many birds and observed them struggle for the prey. It may well be, however, that a bird would be quite willing to swallow a very unsavory mouthful in order to prevent any of its companions from, apparently, enjoying it. However, Beddard found that toads will eat any insect without hesitation in spite of brilliant coloration, strong odors, or stings. He also found that birds and marmosets would often devour "conspicuously colored" larvae without any hesitation, and that some "protectively colored" or inconspicuous larvae were refused. There can be no doubt that many insectivorous animals pay but little attention to the colors of their prey; for example, it is well known to anglers that trout and salmon will snap at the most gaudily colored "flies," which may or may not have any counterpart in nature.

The whole question of warning coloration will have to be made the subject of an extensive research upon both old and young insectivorous animals before we can safely arrive at any certain conclusions respecting it.

II. Methods Pursued in Studying the Color-Patterns of the Heliconidae.

No comparative study of the color-patterns displayed by the Heliconidae has ever been made. In fact, very few such studies have been carried out upon any Lepidoptera. The only works I know of are those of Eimer ('89) and Haase ('92) upon the coloration of the Papilios, and of Dixey ('90) upon the wing-markings of certain genera of the Nymphalidae and Pieridae. The family of the Heliconidae with its numerous species and comparatively simple coloration affords an excellent opportunity for such a research.

In making this study of the Heliconidae I was permitted through the kindness of Mr. Samuel Henshaw to make free use of the collection in the Museum of Comparative Zoölogy at Harvard. I also found the colored figures in the works of the following authors of great service: Hewitson ('56–'76), C. und R. Felder ('64–'67), Hübner ('06–'25), Humboldt et Bonpland ('33), Cramer (1779–'82), Staudinger ('84–'88), Godman and Salvin ('79–'86), and Ménétriés ('63); likewise the following shorter papers published in various serials: Bates ('63, '65), Butler ('65, '69, '69–'74, '77), Druce ('76), Godman and Salvin ('80), Hewitson ('54), Snellenen van Leeuwen ('87), Srnka ('84, '85), Staudinger ('82), and Weymer ('75, '84). I was thus enabled to examine the color-patterns of 400 (89%) of the species of the Danaoid group, and of 129 (86%) of the Acraeoid group, either from the insects themselves or from figures given by the authors named above. The remaining species were either inaccessible to me, or were so vaguely described as to be unavailable. A list of the species known to me is given in Table 28.

(1) *The Two Types of Coloration in the Danaoid Heliconidae.* It is very remarkable that the color-patterns of all of the Heliconidae

may be grouped into two very closely related types. To the one of these I have given the name "*Melinaea type*," for it is characteristic of most of the species of the genus Melinaea. It is well represented by Figs. 46, 48, 49, 51, and 55–57 (Plate **4**). The insects which belong to this type possess wings colored with *rufous*, *black*, and *yellow*.

The other type I designate as the "*Ithomia type*," for it is very characteristic of most of the species of the genus Ithomia. Figs. 47 and 52 (Plate **4**) afford examples of it. This type differs from the Melinaea in that the rufous and yellow areas upon the wings have become *transparent*.

There are, also, many species, found in numerous genera, which fall between these two types of coloration, for the yellow and rufous spots upon their wings have become translucent, so that one may speak of them as "translucent yellow" and "translucent rufous." These spots are, so to speak, in process of becoming transparent, but a few yellow or rufous scales still remain dusted over the otherwise clear spaces. Most of the Dircennas are good examples of this type (Fig. 54, Plate **4**).

Of the 400 species of the Danaoid Heliconidae, about 125 belong to the "Melinaea type." It is well represented by most of the species of the genera Lycorea, Athyrtis, Ceratinia, Mechanitis, and Melinaea. About 30 Ithomias and half a dozen Napeogenes also belong to it. About 160 species belong to the "Ithomia type," and of this number fully 120 belong to the genus Ithomia. The others are found in the genera Ceratinia, Napeogenes, Ituna, and Thyridia, and many of them resemble the Ithomias so closely that they are said to mimic them. About 100 species, some of which are found in almost all of the genera, are intermediate in their color-patterns between the Melinaea and the Ithomia types. The 15 remaining species are represented by Melinaea gazoria (Fig. 53, Plate **4**), Ceratinia eupompe, and a few Ithomias, such as Ithomia hemixantho. In these forms almost all color has disappeared, so that the whole wing has become of a uniform dull translucent yellow, bordered on the outer edges by a grayish black.

(2) *Detailed Description of the Melinaea Type of Coloration.* Figs. 46, 48, 49, 51, and 55–57 (Plate **4**) afford examples of this type of coloration. In these insects we find the proximal half of the central cell of the fore wing occupied by a rufous-colored area, which I call the "inner rufous." It is marked I in all of the figures.

Beyond the "inner rufous" we find a black spot, marked II in the figures. It usually occupies the middle region of the cell of the fore wing, and I have designated it as the "inner black." Beyond the "inner black," and occupying most of the outer portion of the cell of the fore wing, is a light-colored area, marked III in the figures. This area is rufous in color in Fig. 49, but it is usually yellow, as in Figs. 46, 48, 51, 54–57, and I have called it the "inner yellow." Beyond the "inner yellow," and occupying the extreme outer portion of the cell, lies the "middle black" (IV). In many species it is fused, as in Figs. 46–48, 56, 57, with the large black area, the "outer black" (VII), which occupies the greater portion of the outer half of the fore wing. Just outside of the cell beyond the "middle black" one finds a well-developed yellow area (V), the "middle yellow," and there is sometimes still another yellow patch beyond this, which is marked VI and called the "outer yellow." Finally, one often finds a row of white or yellow spots, the "marginal spots" (IX), lying very near the outer margin of the fore wing (see Figs. 47–49, 51, 54, 56). These spots are very well developed in the genera Ceratinia, Napeogenes, Ithomia, and Melinaea. One more very characteristic marking of the fore wing remains to be noticed; that is the longitudinal black stripe (VIII). It is also worthy of note that the front costal edge of the fore wing is almost always tinged with black.

The pattern of the hind wing is quite simple. The ground color is usually rufous and a "middle black" band (XI) runs across the middle of the wing. The outer edge is bordered by the "outer black" (XIII). Above the "middle black" band lies the "inner rufous" (X) of the hind wing, and below the "middle black" band one finds the "outer rufous" (XII) of the hind wing. One often finds a row of white or yellow dots within the outer black border of the hind wing, and these I designate as the "marginal spots" of the hind wing.

The *Ithomia type* of coloration, it will be remembered, may be derived from the Melinaea, by simply imagining the rufous and yellow areas to have become transparent. Also the outer black usually suffers a reduction so as to become only a rather narrow border along the outer margin of the fore wing. Thyridia psidii (Fig. 47) is a good example of this type. It will be seen that the black areas remain about the same as in the Melinaea type, but that the rufous and yellow have become transparent. The middle and outer yellow areas have also fused into a large transparent patch.

Ithomia sao (Fig. 52, Plate **4**) is another good example of the Ithomia type. In this particular species the "inner black" of the fore wing is absent, and the "middle black band" of the hind wing has disappeared. When we come to consider the other Ithomias, we shall find that in this genus it has probably fused with the marginal black of the hind wing.

I have made a record of the color-variations that affect the various characteristic areas just considered, and have recorded them for every one of the species of the Danaoid and Acraeoid Heliconidae known to me. As these records are too extensive for convenient inspection, I have condensed the results, and they will be found in Tables 1–27 inclusive. Thus, Table 1 gives the variations in color of the "inner rufous" area of the fore wing for each genus of the Danaoid Heliconidae; Table 2 records the variations of the "inner black"; Table 3 the "inner yellow" area, etc. In Table 1 we find, for example, opposite the genus Ituna, the number 2 in the column labeled "transparent." This indicates that in two species of Ituna the "inner rufous" area is transparent.

In order to facilitate the study of the color-patterns Dr. Davenport suggested that I make use of the ingenious projection method invented by Keeler ('93). This method consists in "squaring the wing" in the manner shown in Figs. 4 and 5 (Plate **1**). In Fig. 4 the large rectangle (A, B, C, D) just at the right of the figure of the *hind* wing represents a kind of Mercator's projection of the wing itself. The nervures 1^a, 1^b, 2, 3, etc., are represented by the vertical lines 1^a, 1^b, 2, 3, etc., on the rectangle A, B, C, D. In cells I^a, I^b, and I^c, (bounded by nervures 1^a, 1^b, and 2,) one finds a sinuous line winding across the middle of the cell. This line appears in the same relative position upon the rectangle A, B, C, D. The same is true of the eye-spot found in the cell bounded by nervures 2 and 3, and of all the other markings of the wings. The central cell of the wing itself is shown projected in the dotted rectangle E, F, G, H.

In the case of the *fore* wing (Fig. 5), the central cell of the wing is dotted, and is shown projected upon the similarly dotted area within the rectangle I, J, K, L. In other respects the method of projection is the same as in the case of the hind wing.

In this manner the colors displayed by various species of Danaoid and Acraeoid Heliconidae have been represented in color in Plates **5**-**8**. Each large rectangle upon the left hand side of the Plate represents a hind wing, the small middle rectangles show the colors of the cell of the hind wing, and the right hand rectangles give the fore wings, all being projected in the manner illustrated in Figs. 4 and 5, Plate **1**. The chief advantage in Keeler's projection method lies in the fact, that similar areas in the projection of the wings lie vertically under or over one another, and thus by merely glancing up or down the plates one may observe the color-variations which occur in homologous cells of all the species represented.

III. General Discussion of the Color-Patterns and of Mimicry in the Genera Heliconius and Eueides.

Among the species of the genera Heliconius and Eueides we find remarkably little variation in venation, but great diversity in color-pattern of the wings, and in this respect they are very different from the Danaoid Heliconidae, where, it will be remembered, we find fully twenty different types of venation and only two types of color-pattern.

(1) *The Four Color Types in the Genus Heliconius.* Schatz and Röber ('85–'92) divide the species of the genus Heliconius into four groups based on color differences, as follows:—(1) the "Antiochus group" (Plate **4**, Fig. 50); (2) the "Erato group" (Fig. 60); (3) the "Melpomene group" (Fig. 59); and (4) the "Sylvanus group," a good example of which is Heliconius eucrate (Fig. 58, Plate **4**).

It will become apparent through an inspection of Figs. 50, 60, 59, and 58, which represent respectively, Heliconius antiochus, H. erato, H. melpomene, and H. eucrate, that the first three are quite closely related in color-pattern, while the fourth (H. eucrate) approaches very closely to the plan of coloration of the Melinaea type of the Danaoid Heliconidae. In fact this resemblance is so close that it may be safely said that the members of the "Sylvanus group," to which H. eucrate belongs, mimic the Danaoid Heliconidae.

The "Antiochus group" is represented by Heliconius antiochus (Plate **4**, Fig. 50, and Plate **5**, Fig 62). H. sara, H. galanthus, and H. charitonius (Plate **5**, Figs. 61, 63, 64) are also members of this group; other examples are H. apseudes, H. cydno, H. chiones, H. hahnesi, H. sappho, H. leuce, H. eleusinus, and H. clysonymus.

These species are characterized by their blue iridescence, and the narrow yellow or white bands upon the primaries; the hind wings are pointed at the outer apex, and the venation approaches the type found in Eueides aliphera. H. ricini (Plate **5**, Fig. 66) is a good example of a form intermediate in coloration between group 1 and the "Erato group" (2).

The type of group 2 is Heliconius erato (Plate **4**, Fig. 60, and Plate **5**, Figs. 67 and 68). This group is closely allied to group 1 in its characteristics. A good connecting link between groups 1 and 3, the "Melpomene group," is H. phyllis (Fig. 65).

The third, or "Melpomene group," is represented by H. melpomene, H. callicopis, H. cybele, H. thelxiope, and H. vesta (Plate **6**, Figs. 70–74, and Plate **4**, Fig. 59). H. vulcanus, H. venus, H. chestertonii, H. burneyi, and H. pachinus are also examples of this group.

(2) *Mimicry between the Genus Heliconius and the Danaoid Group.* To Schatz's group 4, the "Sylvanus group," belong all those species of Heliconius which have departed widely from the coloration pattern of the other three groups, and have come to resemble various species of the genera Melinaea, Mechanitis, and Tithorea of the Danaoid Heliconidae. H. eucoma, H. eucrate, H. dryalus, and H. sylvana (Plate **8**, Figs. 88, 89, 91, and 95) are good examples of group 4. By glancing at the diagrams on Plate **8** it will be seen that H. dryalus resembles Melinaea paraiya very closely; in fact, the likeness is so close that it is almost certain that no eye could distinguish between the two insects when they are upon the wing. Another startling resemblance is that between H. eucrate and Melinaea thera (Plate **8**, Figs. 91 and 92); moreover, there is but little difference between the color-patterns of H. eucrate, Eueides dianasa, and Mechanitis polymnia (Figs. 91, 93, and 94). H. sylvana and Melinaea egina (Figs. 95 and 96) are also said to mimic each other. The resemblance certainly appears very close at a casual glance, yet when the colors are plotted, as in Figs. 95 and 96, the differences become quite apparent. H. claudia (Plate **5**, Fig. 69) is a good connecting link between the Sylvanus group and the Melpomene group. In both the Melpomene and Sylvanus groups the venation has departed from the Eueides aliphera type, and the contour of the hind wings is much more rounded and elliptical than is the case in the Antiochus and Erato groups. (Compare Figs. 50 and 60 with Figs. 58 and 59, Plate **4**.) There are rather less than twenty species which certainly

belong to the Sylvanus group; among them may be mentioned, in addition to those already spoken of, Heliconius numata, which resembles Melinaea mneme and Tithorea harmonia; H. zuleica, which resembles a Mechanitis and is a good copy of Melinaea hezia; and H. metalilis, which is said to mimic Melinaea lilis; there are also striking resemblances between

H. aurora and Melinaea lucifer;
H. eucrate and Mechanitis lysimnia;
H. hecuba and Tithorea bonplandii;
H. formosus and Tithorea penthias;
H. telchina and Melinaea imitata;
H. messene and Melinaea mesenina;
H. hecalesia and Tithorea hecalesina;
H. ethra and Mechanitis nesaea;
H. pardalinus and Melinaea pardalis;
H. ismenius and Melinaea messatis.

Most remarkable of all perhaps is the close resemblance between Heliconius aristiona, Mechanitis methone, and Ithomia fallax of Staudinger. In fact, Staudinger states in his "Exotische Schmetterlinge" that he hesitated for some time to describe Ithomia fallax on account of its close resemblance to Hewitson's Mechanitis methone. Good lists of the Heliconidae which are said to mimic one another are given by Wallace ('89, p. 250, 251), and by Haase ('93^{a}, p. 146, 147).

(3) *The Three Color-Types in the Genus Eueides.* In the genus Eueides we meet with three color-types represented by E. aliphera, E. thales, and E. cleobaea. These insects are distinctly smaller than the species of the genus Heliconius, and the yellow spots upon their primaries are more ocherous in color than in Heliconius. E. aliphera (Plate **6**, Fig. 77) represents the most highly specialized color-type. Eueides mereaui (Fig. 76), however, is a good connecting link between the color-patterns of E. aliphera and E. thales (Fig. 75), and E. thales is almost identical in color-pattern with Heliconius vesta (Fig. 74).

The other type of Eueides is represented by E. cleobaea, E. dianasa, E. isabella, etc. (Plate **6**, Fig. 78, and Plate **8**, Fig. 93). These resemble the Sylvanus group of Heliconius or various Melinaeas and Mechanitis.

(4) *Detailed Discussion of Plates* **5–8**. PLATE **5** is intended to illustrate the types of coloration found in the Antiochus and Erato groups of the genus Heliconius. In H. sara (Fig. 61) the wings are suffused with a dark blue iridescence, and some narrow yellow bands of color are found upon the primaries. In H. antiochus (Fig. 62) we find similar bands of color upon the primaries, but they are changed to white. H. antiochus may have descended

from an albinic sport of H. sara. In H. galanthus (Fig. 63) the white areas have greatly increased in size, and the iridescent blue has become much lighter. In H. charitonius (Fig. 64) we find the wings crossed by yellow spots and bands, but in some specimens this yellow color exhibits a decidedly reddish tinge. The figure of H. charitonius in Staudinger's "Exotische Schmetterlinge" illustrates this peculiarity; indeed, spots which are commonly yellow are often found red, and *vice versa*. In H. phyllis (Fig. 65) we find along the upper part of the diagram of the hind wing a yellow marking, and a similarly shaped red mark is found in its near ally, H. thelxiope (Fig. 73, Plate **6**). The same is also true of H. ricini (Fig. 66, Plate **5**).

H. erato (Figs. 67 and 68, Plate **5**, and Fig. 60, Plate **4**) is very remarkable, for there are no less than four distinct color-types exhibited by different individuals of this species; one of them (Fig. 67) shows the basal half of the hind wing marked by six red tongues of color edged with iridescent blue, and there is a dark rufous suffusion upon some parts of the fore wing. In other specimens (Fig. 68) the red tongues of color which characterized the hind wing of Fig. 67 are almost absent, and only the blue iridescence is left; also there is no rufous to be seen upon the fore wing. In another type the blue iridescence of the hind wing has become green, and in still other specimens the yellow stripes upon the fore wing have become white.

As one looks over the diagrams upon Plates **5–8**, it becomes evident that yellow frequently changes to white, for we often find one or two species of a genus which exhibit white spots identical in shape and position with spots which are yellow in most of the others. Good examples of this are H. antiochus (Plate **5**, Fig. 62), Melinaea parallelis and Ceratinia leucania (Plate **7**, Figs. 82 and 83); likewise the white spot near the outer apex of the fore wing in H. eucrate (Plate **8**, Fig. 91), which is yellow in many individuals. Yellow areas are also frequently changed to rufous or red; thus the yellow basal half of the hind wing of H. eucrate (Plate **8**, Fig. 91) is often found of a rufous tinge in individual specimens of the species, and among the specimens of this species in the Museum of Comparative Zoölogy one can trace a gradation of this area from bright yellow to rufous. H. claudia (Plate **5**, Fig. 69) is introduced in order to exhibit some of the differences between the "Sylvanus" group, to which it belongs, and the "Antiochus" and "Erato" groups.

Plate **6** is intended to exhibit the characteristic color-patterns found in the Melpomene group and in the genus Eueides. Fig. 70 represents H. melpomene, and Fig. 71 its near ally, H. callycopis, in which the red area of the fore wing has become broken up, and some red spots have made their appearance near the base of the hind wing. In the next variety of H. melpomene, H. cybele (Fig. 72), it is remarkable that the pattern of the fore wing has come to resemble the Sylvanus type, and is identical in general plan of coloration with the fore wings of the Melinaeas or Mechanitis (see Figs. 84 or 85, Plate **7**, or Figs. 92 or 94, Plate **8**). In its close ally, H. thelxiope (Fig. 73), a still nearer approach to the Melinaea type has come about by the development of a black band across the middle of the hind wing, and one has only to imagine a general fusion of the seven club-shaped red stripes of the hind wing in Fig. 73, Plate **6**, in order to produce exactly the Melinaea type as exhibited, for example, by Eueides cleobaea (Fig. 78). In this connection it is worthy of note that Bates ('62) showed that H. thelxiope was derived from H. melpomene, there being between the two many intermediate forms.

H. vesta (Fig. 74) is evidently a close relative of H. thelxiope, and what is still more worthy of note is, that it is almost identical in the general effect of its color-pattern with Eueides thales (Fig. 75)! The yellow spots upon the fore wing of E. thales are, however, duller in hue than are those of H. vesta, and the insects are somewhat different in size, H. vesta spreading 78 mm., while E. thales spreads only 66 mm. It will be noticed that the chief difference between the color-patterns of these two species lies in the fact, that, while the black stripes of the hind wings in H. vesta lie along the nervures, in Eueides thales they occupy the middle of the cells themselves. The general resemblance of the two color-patterns may of course be merely accidental. An easy explanation, however, is afforded by the theory of mimicry, for the two species look very much alike until one subjects their color-patterns to close analysis, when remarkable differences appear. E. thales (Fig. 75) may have been derived from some such form as E. mereaui (Fig. 76), for one has merely to imagine a greater development of the black and a general deepening of the rufous upon the hind wing of E. mereaui to make it resemble E. thales quite closely. Finally, in E. aliphera (Fig. 77) the black serrated border of the hind wing is still more reduced, and the black stripe which crosses the cell of the fore wing in E. mereaui is not present.

Plate **7** is intended to illustrate the peculiarities of color-pattern found among the Danaoid Heliconidae. Thyridia psidii (Fig. 79) is an example of the transparent type of color-pattern found among the Danaoid Heliconidae, and especially prevalent among the Ithomias. It will be seen by comparing Fig. 79 with the other figures upon Plates **7** and **8**, that the chief difference lies in the fact, that in this type both the rufous and yellow areas have become transparent. The black area of the fore wing has also suffered a reduction, especially along the outer margin of the wing. Incidentally it should be mentioned, that in this *particular* species the middle black band of the hind wing has become tilted up at a sharp angle, instead of crossing the wing horizontally. A life-size figure of the wings of Thyridia psidii is given on Plate **4**, Fig. 47.

In Napeogenes cyrianassa (Fig. 80) and Ceratinia vallonia (Fig. 81) portions of the usually yellow and rufous areas have become transparent.

The spots upon the fore wing of the Melinaeas are usually yellow, but in Melinaea parallelis (Fig. 82) they are white. It would seem that this form may have descended from some albinic sport. Ceratinia leucania (Fig. 83) resembles Melinaea parallelis so closely in general plan of coloration, that it is very difficult to distinguish between them, even when the two insects are seen side by side. Ceratinia leucania, however, is somewhat smaller than Melinaea parallelis. Both occupy the same region in Central America, and the specimens from which the diagrams were drawn came from Panama.

Figs. 84–87 are drawn from various specimens of Mechanitis isthmia, all from Panama. They are intended to give some idea of the range of individual variation which is met with in this extremely variable form. The contraction of the middle black band of the hind wing in this form has already been noticed in the general discussion of the laws of color-pattern (see page 184). In Fig 87 it will be seen that the inner yellow stripe which usually crosses the cell of the fore wing has become very narrow and changed to a rufous color. However, upon the under surface of the wing it still remains as a yellow stripe. Indeed, in most color-changes the upper side of the wing seems to take the initiative, the under surface being more conservative. This is not true, however, in the Ithomias, where the black areas of the under side of the wings often are found to be rufous in color, while they still remain of the normal black upon the upper surface. The colors of the under surface are, however, usually identical with those of the upper, though they are always *duller in hue.* This may be due to the fact, that the colors of the upper surface are more frequently seen than those of the lower, for these insects often float lazily along with their wings horizontally extended. The operation of Natural Selection would then be more severe with the upper surfaces than with the lower.

PLATE **8** gives an analysis of the color-patterns of some of the Heliconinae and those Melinaeas, etc., which they resemble. H. eucoma (Fig 88) is a good example of the Sylvanus type, and with its rufous, yellow, and black wings it is certainly a wonderfully close copy of the color-pattern found so commonly among the species of the genus Melinaea of the Danaoid Heliconidae.

Heliconius dryalus and Melinaea paraiya (Figs. 89, 90) resemble each other so closely in size, shape, and coloration, that it must be impossible to distinguish between them when the butterflies are in flight; yet an analysis of their color-patterns shows that there are considerable differences between them. The shape of the yellow bands upon the fore wings is quite different; the inner black spot within the cell is double in Melinaea paraiya, and there is also a row of white spots along the margin of the fore wing.

A much closer resemblance is found between H. eucrate and Melinaea thera (Figs. 91 and 92), where the Heliconius is almost a true copy of the Melinaea.

The color-patterns of Eueides dianasa (Fig. 93) and Mechanitis polymnia (Fig. 94) are also very nearly the same. Both are common species in Brazil.

Heliconius sylvana is said by Bates and by Wallace to mimic Melinaea egina. It will be seen by reference to Figs. 95 and 96 that their color-patterns are quite different in detail, yet the insects look very much alike when placed side by side, and may easily be mistaken for each other when upon the wing. Melinaea egina is much more common than Heliconius sylvana.

IV. GENERAL DISCUSSION OF THE COLOR-PATTERNS AND OF MIMICRY AMONG THE DANAOID HELICONIDAE.

(1) *The Origin of the Two Types of Coloration.* The character of the variation in the Danaoid Heliconidae is very different from that of the genera Heliconius and Eueides, for while there is great

diversity of color-pattern and very little variation in venation among the species of the Acraeoid group, exactly the opposite condition is met with in the Danaoid group, where we find at least twenty different types of venation and only two types of color-pattern. One of these types of coloration is well exemplified by most of the Melinaeas (Fig. 48, Plate **4**), and I have therefore called it the "*Melinaea*" type. The other type is exemplified by most of the Ithomias (Figs. 47 and 52) and has been designated in this paper as the "*Ithomia*" type. In the Melinaeas, it will be remembered, we find the rufous and black wings crossed by bands of yellow; while in the Ithomias, on the other hand, the rufous and yellow areas have become transparent, often leaving the wing as clear as glass, and the black, which is so characteristic of the outer half of the wing in the Melinaea type, has shrunk away until it has come to lie along the outer margin of the wing only.

By a study of all the genera of Danaoid Heliconidae we gain light upon the question of the origin of the "Melinaea" and "Ithomia" types of coloration. As we have seen (page 198), the Danaoid Heliconidae are an offshoot from the great family Danaidae. Indeed, two of the genera, Lycorea and Ituna, are so closely related to the Danaidae that Schatz and Röber ('85–'92) propose to include them within that family. There can be but little doubt that Lycorea and Ituna are remnants of the ancestral forms which long ago shot off from the Danaidae to form the Danaoid Heliconidae: and it is interesting to note, that in these two patriarchal genera we find the two distinct types of color-pattern which are exhibited by the Danaoid Heliconidae, for all of the five known species of Lycorea are good examples of the Melinaea type (see Lycorea ceres, Fig. 46, Plate **4**), while the four known species of Ituna all exhibit the transparent, or Ithomia, type of coloration. In fact, in their color-patterns the species of Ituna remind one of gigantic Ithomias. The species of Lycorea, however, are colored very much after the pattern of the Danaidae, and indeed they have departed but little from the type of the members of the great family whence they sprang. On this account I believe that the Melinaea type of coloration, which is so characteristic of the species of Lycorea, is phylogenetically older than the Ithomia type.

In order to account for the origin of the Ithomia type, we may assume that, shortly after the primeval forms of the Danaoid Heliconidae began to segregate out from the Danaidae, the species were few and probably rare. Under these circumstances any given insect would gain but little advantage by resembling merely the general type of the coloration of its fellows. For the relative advantage gained by such imitation, according to Fritz Müller's law, increases inversely as the square of the fraction whose numerator is the actual number of the imitating form and whose denominator is the actual number of the imitated. Therefore when the insects were still rare there would be few to imitate and consequently but little advantage would be gained by the imitation. Imagine, for example, that a single insect happens to imitate the color-pattern of a group of 100, and that the advantage gained thereby is represented by the number 1; it is evident from Fritz Müller's law that, if it happened to imitate the coloration of a group of 1,000, its relative advantage would be 100 instead of 1. We see, then, that mimicry within the group of the Danaoid Heliconidae became an important factor only after the group was well established and the insects became common. During the early history of the race, then, there would be but little tendency towards conservatism of color-patterns, and when the "Ithomia" and "Melinaea" types of coloration made their appearance, they both survived and now serve as the patterns for mimicry; and this accounts very well for the remarkable fact, that there are no other types of coloration than these two to be found within the whole group with its 450 species!

(2) *Mimicry among the Danaoid Heliconidae.* The genus Ithomia with its 230 species is the dominant genus of the Danaoid group, and in nearly all of the other genera individual species are found which have departed widely from their generic type of coloration and have assumed the clear wings of the Ithomias. A good idea of how far these interesting individuals may depart from the coloration of their type may be gained by comparing Fig. 53, Plate **4**, which represents Melinaea gazoria, with Fig. 48, which represents a typical Melinaea (M. paraiya). It is evident that Melinaea gazoria is startlingly like an Ithomia both in size and coloration, although it retains the venation and generic characteristics of a Melinaea.

In Mechanitis, which is the most independent genus of the Melinaea type of coloration, all of the species are fair examples of the Melinaea type, except Mechanitis ortygia Druce, from Peru. Druce ('76) in his description of this curious little species states in astonishment that it possesses the venation of a Mechanitis, but the size and coloration of an Ithomia!

It is quite remarkable that although the genera Melinaea and Mechanitis serve as models of mimicry for the Acraeoid Heliconidae, they should themselves mimic Ithomia.

The genus Ithomia is, however, the most independent of all the genera of the Danaoid group, and I know of remarkably few good instances in which an Ithomia has apparently departed from the coloration of its type to assume the guise of the Melinaeas. One good example of such a change, however, is afforded by Ithomia fallax of Southern Peru, which resembles either Mechanitis methone or Heliconius aristiona of Colombia (see page 210). There is apparently a difficulty in ascribing this resemblance to mimicry, for the imitator and imitated do not occupy the same geographical regions.

In direct contrast with the independence of the Ithomias stands the case of the genus Napeogenes; for Godman and Salvin ('79–'86) say of Napeogenes, that nearly every species mimics some Ithomia which occupies the same district; and thus almost the very existence of the genus would seem to depend upon its mimicry of Ithomia.

It is not the purpose of this paper to discuss, in detail, the numerous interesting cases of mimicry which are believed to exist between members of the Danaoid Heliconidae. An excellent discussion of such cases, and of the relationships of the various genera, has been given by Haase ('93^a, p. 116–127).

V. Quantitative Determination of the Variations of the characteristic Wing-Markings in the Acraeoid and Danaoid Heliconidae.

(1) *Variations of "Inner Rufous" Areas of the Fore and Hind Wings.* Table 1 gives the color-variations which are exhibited by the "inner rufous" area of the fore wings in the Danaoid Heliconidae. This area is marked I in all of the figures upon Plate **4**. We learn from an inspection of Table 1 that this area is rufous in color in 124 species of the Danaoid Heliconidae, transparent in 152, black in 24, and that in the remainder it is more or less translucent, and of either a yellowish or rufous tinge.

Table 10 shows the variations which come over the "inner rufous" area of the hind wings of the Danaoid Heliconidae. This area is marked X in the figures upon Plate **4**. It is apparent at a glance that the variations which affect the inner rufous areas of both fore and hind wings are very similar. In order to exhibit this fact graphically, the color-variations have been laid off upon the diagram, Fig. 97, Plate **9**. The base line is marked at equal intervals with the words "rufous," "translucent rufous," "translucent, slightly rufous," "transparent," etc., and the ordinates show the number of species which exhibit the various colors, rufous, translucent rufous, etc. For example, at the point "translucent rufous" we find that the ordinate is 23; this indicates that in 23 species the area is translucent rufous in color. The points thus found upon the ordinates are successively joined by straight lines forming a zig-zag figure. The full line represents the fore wing, and the dotted line the hind wing, and it becomes clearly evident from the closeness of these two zig-zag lines that the color of the inner rufous area of the fore wing (area I, Plate **4**) is almost always sure to be identical with that of the inner rufous area of the hind wing (area X, Plate **4**). We see, therefore, that whatever color-variation affects the inner rufous area of the fore wing, this area in the hind wing is almost always affected in the same manner.

Fig. 99, Plate **9**, is derived from Tables 15 and 24, which show the color-variations in the fore and hind wings of the genera Heliconius and Eueides. It is seen that here also the colors of these two areas in both the fore and hind wings are almost always identical. We here meet with one of those interesitng physiological laws which are independent of Natural Selection, and the meaning of which remains a mystery, for surely we can see no reason on the ground of adaptation why similar areas upon both fore and hind wing should bear similar colors.

(2) *The "Inner Black" Spot.* Table 2 shows the presence or absence of the "inner black" spot in the Danaoid Heliconidae. This spot is marked II in the figures upon Plate **4**. When present, it is always black in color and is usually found occupying the middle region of the cell of the fore wing. The table shows that it is about an even chance whether it be present or not, for it is absent in 210 species and present in 190. In the genus Ithomia, however, it is present in only one third of the species. What is most worthy of note concerning it, is the fact that it almost always appears, when present, as a single spot. Indeed, it appears as a double spot in only 7 species, and 5 of these belong to the genus Melinaea. A good example of its appearance as a double spot is found in Melinaea paraiya (Fig. 48, Plate **4**). It will be remem-

bered that there are 450 species in the Danaoid group; 25 of these belong to the genus Melinaea; yet among these 25 we find 5 exhibiting this marking as a double spot. Assuming that the doubling of this spot has arisen in each species as a sport, and that such a sport is as likely to appear in one species as in any other of the Danaoid group, then the chances against five such sports appearing among the 25 Melinaeas is $\frac{450\times449\times448\times447\times446}{25\times24\times23\times22\times21}$, or about 2,830,000 to 1. Indeed, it is probable that all five of the species of Melinaea which exhibit the doubling of this spot are descendants of a *single* ancestor in which it appeared for the first time double, for the mathematical chance that one such ancestor should appear among the Melinaeas, rather than in any other genus, is evidently 1 in $\frac{450}{25}$, or one chance in eighteen. The chance against two such unrelated ancestors is, however, $\frac{450\times449}{25\times24}$, or about 336 to 1, and the chance against three is $\frac{450\times449\times448}{25\times24\times23}$, or 6,560 to 1, etc.

By reference to Table 16 we find that in the genera Heliconius and Eueides the inner black area is black or iridescent blue in all of the species of Heliconius, but absent in 5 of the 18 species of Eueides known to me. These 5 include Eueides aliphera and its allies. Now there are 150 known species of the Acraeoid Heliconidae, and 24 of these belong to the genus Eueides; so it is evident that the mathematical chance against the supposition that five sports arose independently in the genus Eueides, in which the inner black was absent, is given by $\frac{150\times149\times148\times147\times146}{24\times23\times22\times21\times20}$, or 13,900 to 1. It is therefore probable that the five Eueides lacking the inner black are the descendants of a single ancestor.

(3) *Variations of the "Inner Yellow" and "Middle Yellow" Areas.* Tables 3 and 5, and diagram Fig. 98, Plate **9**, show the color-variations of the "inner yellow" and "middle yellow" areas in the fore wings of the Danaoid Heliconidae. These areas are marked III and V, respectively, in the figures upon Plate **4**. The "inner yellow" area, it will be remembered, occupies the outer portion of the cell of the fore wing; while the "middle yellow" is found in the region just beyond the outer limits of the cell. The two areas are often fused together as in Figs. 47, 48, 50, 51, and 55, Plate **4**. The inner yellow area is usually smaller than the middle yellow, and a comparison of Tables 3 and 5 will show that it is much more frequently obliterated by the encroachment of the rufous or black

areas which surround it; for example, while the middle yellow is rufous in color in only 14 species, the inner yellow is rufous in 56; also the inner yellow area, being usually smaller and less conspicuous than the middle yellow, is less important in cases of mimicry, and the diagram Fig. 98, Plate **9**, shows that it is much more variable in color than the middle yellow. The full zig-zag line in this figure represents the color-variations of the inner yellow, while the dotted zig-zag line gives the color-variations of the middle yellow. As there are nine color-variations displayed by each of these two areas, and as there are 400 species of the Danaoid Heliconidae recorded by me, it becomes evident that, if there *were* no color preferences displayed by these areas, there would probably be about $\frac{400}{9}$, or 44.4, species which would display it as rufous, 44.4 translucent, 44.4 yellow, etc. The heavy, straight, dotted line (Fig. 98, Plate **9**) represents this ideal condition, which would be approximately realized were one color as likely to occur as another in the respective areas. Now it is evident from an inspection of the figure, that the full zig-zag line, which represents the color-variations of the "inner yellow," approaches the straight line condition more nearly than does the dotted zig-zag line, which represents the middle yellow.[1] The inner yellow is therefore more liable to color-variations than the middle yellow; and this is what we should expect on account of its comparatively small size and its consequent inconspicuousness as a characteristic marking in cases of mimicry.

A comparison of Figs. 97 and 98, Plate **9**, is interesting, for it shows that the color-variations of the inner rufous are quite similar to those of the inner yellow and middle yellow. This serves to illustrate the close physiological relationship which exists between rufous and yellow. The two pigments are probably closely related chemically, for every ordinarily rufous area is sometimes found to be yellow, and *vice versa*. Yellow areas also often change to white. Rufous, yellow, and white are evidently closely related color-variations.[2]

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[1] This is not true for one color, white.

[2] It may be well to mention here that the black areas upon the wings are subject to very little color-variation. In some cases, however, especially upon the under surfaces of the wings in Ithomia, the black has changed to a rufous or russet color. For example, Table 4 shows that the middle black area (IV in the figures upon Plate 4) is rufous in only 12 species out of the 400 which are recorded, and all of these 12 are Ithomias. Also Tables 7 and 13 show that the outer black of the fore wing, and the outer black of the hind wing are russet in 22 and 11 species, respectively. Evidently, black is a far more conservative color than rufous, yellow, or white. Probably black is also quite different from the other pigments chemically.

Tables 17 and 19 show the color-variations affecting the "inner yellow" and "middle yellow" areas of the fore wing in Heliconius and Eueides. There is but little difference between the two tables, except that in 15 species of Heliconius the inner yellow is suffused with black or blue, while the middle yellow is never suffused by the outer black which surrounds it. Fig. 100, Plate **10**, exhibits graphically the color-variation of these two areas. The "inner yellow" is represented as a full line, and the "middle yellow" as a dotted zig-zag. It is evident that here also the inner yellow is more variable in color than the middle yellow, for not only does the inner yellow area display two more colors, but its chart is a flatter zig-zag.

(4) *Variations of the "Middle Black" Mark of the Fore Wing.* Table 4 shows the color-variation of the middle black mark (area IV in figures upon Plate **4**). This marking lies along the extreme outer border of the central cell of the fore wing. It is small in area, but is rendered very conspicuous from the fact that it is situated between the inner yellow and middle yellow markings. In spite of its small size, however, it is a remarkably permanent marking, for Table 4 shows that it is absent in only 20 out of 400 Danaoid Heliconidae. In these 20 it has been obliterated by the fusion of the inner and middle yellow areas. It is worthy of note that in 12 Ithomias it has become rufous in color. This change to rufous is the only color-change which the black areas of the wings ever display.

Table 18 shows the variations of the middle black area for Heliconius and Eueides.

(5) *Variations of the "Outer Yellow" Area of the Fore Wing.* Table 6 shows the variations which affect the outer yellow area of the fore wings in the Danaoid Heliconidae. This area is marked VI in the figures upon Plate **4**; it lies beyond the region of the middle yellow, but is usually more or less fused with it. Table 6 is only approximately correct, owing to the difficulty in many cases of deciding whether the middle and outer yellow be really fused or not. It will be seen that in the genus Ithomia the middle and outer yellows are wholly fused in about 200 species. This is one of the marked characteristics of this very independent genus.

Table 20 shows the color-variations of the outer yellow area in Heliconius and Eueides. This marking is present in 81 and absent in 48 of the Acraeoid group. It is much more widely separated from the middle yellow than is the case in the Danaoid group.

(6) *The relative Permanency of the Black Areas upon the Fore and Hind Wings.* A study of the relative permanency of the various characteristic black markings upon the wings is of interest, for, if the generally accepted idea concerning the prevalence of mimicry within the group of the Danaoid Heliconidae be true, we should expect the most conspicuous markings to be the most permanent, for they are evidently of the most importance for mimicry. This is, however, not the case for the black markings. A good example of this fact is afforded by a comparison of the relative permanency of the black streak which extends along the extreme costal edge of the fore wing with the inner black spot (II in figures on Plate **4**). The inner black spot is certainly a more conspicuous marking than this narrow black streak along the costal edge; yet it is much more variable, for Table 2 shows that it is present in 210 and absent in 190 of the 400 Danaoid Heliconidae. In other words, it is about as likely to be present as absent. The black streak upon the costal edge, on the other hand, is much more permanent, for it is absent in only 52 species out of the 400.

Another good example of the inaccurracy of the supposition that large and conspicuously colored areas are always less variable than small ones, is derived from a comparison of the relative variability of the large outer black of the fore wing with the small outer black of the hind wing. Although the outer black area of the fore wing is usually much larger and more conspicuous than the outer black margin of the hind wing, it is more variable in color, for it is rufous in 22 species, while the outer black of the hind wing is rufous in only 11, out of the 400.

In general, however, large colored areas are more permanent than small ones, as was found in the case of the inner and middle yellow areas (see page 220). Indeed, a good instance of this greater variability of small color areas is afforded by the longitudinal black stripe marked VIII in the figures of Plate **4**, for this is more variable than the larger outer black area of the fore wing.

(7) *The "Middle Black Stripe" of the Hind Wing.* In the genus Ithomia the middle black stripe (XI, Plate **4**) has migrated downward, so that in many species it has become fused with the outer black margin, as in Ithomia sao (Fig. 52, Plate **4**). In other cases there is still to be seen a narrow line of rufous color between the middle black band and the outer black margin of the hind wing. Such is the case in Ithomia nise (Fig. 54, Plate **4**). In

many other cases the outer black and middle black are completely fused, so far as the upper surface of the wings is concerned; but, if one examines the under surface of the hind wings, it will be found that a narrow rufous streak still persists between the middle black band and the outer black margin of the hind wing.

(8) *Variations of the Marginal Spots of the Fore Wing.* The marginal spots are found very near the outer margin of the fore wing; they are usually either yellow or white, but in some few cases they are rufous. It appears from Table 9 that they are present in 146 and absent in 254 species of the 400 Danaoid Heliconidae known to me. Fig. 101, Plate **10**, shows graphically the manner in which these spots occur in those species which possess them. It is evident from this curve that the number of these spots is not determined merely by chance, for they show a marked tendency to appear either as 2 or 3, or as 6 or 7 spots. It is due to this fact, that there are two maximum points upon the diagram Fig. 101, Plate **10**. In those species which exhibit the "2- or 3-spot" condition, the spots are found near the front apex of the fore wing. In the "6- or 7-spot" condition they lie all along the outer margin of the fore wing, one spot in each cell. In the genera Ithomia, Napeogenes, and especially in Ceratinia these marginal spots have become large and conspicuous ornaments. (See Fig. 49, Plate **4**.)

Table 22 shows the manner of appearance of these spots in the genera Heliconius and Eueides. They are found in only 26 species of the 129 known to me; and this number is far too small to warrant general conclusions concerning the order of their appearance.

(9) *The Marginal Spots of the Hind Wing.* Table 14 illustrates the manner in which the marginal spots of the hind wings make their appearance. They are absent in 279 and present in 121 of the 400 species of the Danaoid group. Thus they occur rather less frequently than the marginal spots of the fore wing. In the 121 species in which these spots are found they show a decided tendency to appear either as 4 or as 5 spots. Fig. 102, Plate **10**, is a graphic representation of the distribution of these spots, derived from Table 14. It appears that the outline of the figure approaches a probability curve, and is approximately symmetrical about the mean ordinate (A, B), situated at 4.54.

VI. Comparison of the Color–Variations of the Papilios of South America with those of the Heliconidae.

In order to emphasize the peculiarities of the coloration of the Heliconidae, I will conclude by instituting a comparison between their variations and those of the South American Papilios. There are about 200 species of Papilio in South America, and these display in all 36 distinct colors. The colors have been determined by reference to the plates in Ridgway's "Nomenclature of color for naturalists." A list of the colors which are displayed by these Papilios has already been given upon page 191.

By exercising a very fine discrimination in distinguishing color we may count 15 distinct colors which are displayed by the 450 members of the Danaoid Heliconidae, as follows: black, brown, translucent black, sulphur-yellow, canary-yellow, citron-yellow, primrose-yellow, yellow-rufous, reddish rufous, rufous, white, translucent yellow, translucent rufous, transparent areas upon the wings, transparent areas which display iridescence. We see, then, that while the 200 species of Papilio display 36 different colors, the 450 Danaoid Heliconidae exhibit only 15. In other words, the *numbers* of the *species* and of the *colors* are almost in inverse ratio in the two groups; for while the Papilios are only $\frac{4}{9}$ as numerous as the Danaoid Heliconidae, they display almost $\frac{10}{4}$ times as many colors; and this is all the more remarkable when we remember that the general class of coloration in the Papilios and Danaoid Heliconidae is apparently the same. That is to say, in both groups we find all of the species displaying decidedly conspicuous colors, the coloration of the upper surfaces of the wings being in both rather more brilliant than that of the lower surfaces, but without essential differences in color-pattern. Nor is there an attempt in either case at protective resemblances, such as the imitation of the coloration of bark, leaves, etc. The color-patterns of the Papilios are, moreover, extremely complex, and upon comparing the different species, there are seen to be frequent fusions and obliterations of the characteristic markings, so that Haase ('93), who has made an extensive study of their color-patterns, is forced to divide them into many small groups of a few species each. The variation in the form of the wings is also very great among the Papilios, for while P. protesilaus possesses upon its hind wings, long tail-like appendages, the hind wings of P. hahneli are rounded off and without marked appendages.

There is, apparently, but one important respect in which the Danaoid Heliconidae are more variable than the Papilios, and that is size. For example, Lycorea ceres, which is probably the largest of the Danaoid group, has 2.2 times the spread of wing of Ithomia nise, which is one of the smallest (see Plate **4**, Figs. 46 and 54). The largest Papilio, P. androgea, on the other hand, spreads only 2.16 times as much as the smallest, P. triopas.

There is another minor respect in which the color-patterns of the Papilios are different from those of the Heliconidae. In the Heliconidae the fore wing slightly overlaps the hind wing, and that portion of the hind wing which is hidden from view is always dull in color (see Plates **5–8**). In the Papilios, however, the fore wing does not overlap the hind wing to such an extent as in the Heliconidae, and it is worthy of note that the costal edges of the hind wings in the Papilios are as brilliantly colored as are any other portions of the wings.

It is difficult to account for the remarkable conservatism in respect to color-variations among the Heliconidae, unless we resort to the explanation afforded by the theory of mimicry; for, while there is such remarkable simplicity and uniformity of color-pattern throughout the whole group of the Heliconidae, *individual variations* are very common. In the collection at the Museum of Comparative Zoölogy, for example, one finds a regularly graded series of specimens of Heliconius eucrate; at one end of this series the "inner rufous" area of the hind wing is bright yellow, and at the other end it is rufous; intermediate specimens are found in which this area is yellow, but dusted over with rufous scales. Also the "middle black band" of the hind wings in Melinaea parallelis is very variable, some specimens showing it broken in the middle (Plate **7**, Fig. 82), and others having it as an entire band. I have also seen one specimen of H. burneyi in which the commonly yellow spots upon the under surface of the wings were changed to white. Another good instance of individual variability is afforded by H. phyllis (Plate **5**, Fig. 65), for in this species the series of small red spots sometimes found just below the yellow band upon the hind wing is very variable, and more often absent than present. Still other instances of individual variability are seen in the yellow stripes upon the wings of H. charitonius (Plate **5**, Fig. 64), which are often found tinged with rufous. Also the remarkable diversity in Mechanitis polymnia, and M. isthmia (Plate **7**, Figs. 84–87) are other examples which show that there is no lack of individual variability among the Heliconidae. Yet the Danaoid species as a whole vary but little from the two great types of coloration represented by Ithomia and Melinaea, and in this respect they are very different from the Papilios, where we find a great many color-types and great diversity in shape of wings. Surely there must be some cause for the remarkable fact that the Danaoid Heliconidae with their 453 species should display but two types of color-pattern. I can think of but one explanation, which is afforded by Fritz Müller's theory of mimicry.

In conclusion it gives me pleasure to thank those friends whose generous aid and kindness have done so much to render the prosecution of this research a pleasure to me. I wish to express my gratitude to Dr. Charles B. Davenport, who is the real instigator and promoter of this research; to Mr. Samuel Henshaw, to whom I am indebted for numerous kindnesses, and who placed at my disposal the extensive entomological collections and library of the Museum of Comparative Zoölogy at Harvard; to Prof. Edward L. Mark for his kindness in revising the manuscript of this paper, and for the numerous valuable suggestions which he has made; to Dr. Samuel H. Scudder, to whom I am grateful for much kind advice and for the use of rare works in his library; to Prof. Ogden N. Rood for his valuable suggestions in regard to the spectroscopic apparatus; to Dr. Alpheus Hyatt for his valued and kind advice, and to my father, Prof. Alfred M. Mayer, for the use of Maxwell's discs and the direct-vision spectroscope.

PART C.

GENERAL SUMMARY OF RESULTS BELIEVED TO BE NEW TO SCIENCE.

(1) The great majority of the colors of Lepidoptera contain a surprisingly large percentage of black (p. 172).

(2) The colors displayed by the scales are not simple, but compounded of several different colors (p. 173).

(3) The pigments of the scales of Lepidoptera are derived by various chemical processes from the blood, or haemolymph, of the

pupa. The pupal blood of the Saturnidae is a proteid substance containing egg albumen, globulin, fibrin, xanthophyll, orthophosphoric acid, iron, potassium, and sodium (p. 176).

(4) In Callosamia promethea and Danais plexippus the pupal wings are at first perfectly transparent, then white, then impure yellow, excepting upon those portions which are destined to remain white in the mature wing. The mature colors then begin to appear near the central areas of the wings and *between* the nervures. Last of all, the nervures themselves become tinged with the mature colors. The central portions of the wings acquire their mature colors before the outer and costal edges, or the root of the wing adjacent to the body (p. 178, Plate **3**).

(5) The white stage in the development of color in the pupal wings represents the condition in which the scales are perfectly formed but lack the pigment which is destined to be introduced later (p. 178). (See, also, Mayer, '96, p. 230.)

(6) Dull ocher-yellows and drabs are, phylogenetically speaking, the oldest pigmental colors in the Lepidoptera. The more brilliant colors, such as bright yellows, reds, and pigmental greens, are derived by complex chemical processes and are, phylogenetically speaking, of recent appearance (p. 178). (See, also, Mayer, '96, p. 232.)

(7) While the number of species of Papilio in South America is 9 times as great as in North America, the number of colors which they display is only twice as great. Hence the greater number of colors displayed by the tropical forms may be due simply to the far greater number of the species, and not to any direct influence of the climate (p. 191).

(8) The following laws control the color-patterns of butterflies and moths: (a) Any spot found upon the wing of a butterfly or moth tends to be bilaterally symmetrical, both as regards form and color; and the axis of symmetry is a line passing through the center of the interspace in which the spot is found, parallel to the longitudinal nervures (p. 183). (b) Spots tend to appear not in one interspace only, but in homologous places in a row of adjacent interspaces (p. 183). (c) Bands of color are often made by the fusion of a row of adjacent spots, and, conversely, chains of spots are often formed by the breaking up of bands (p. 183). (d) When in process of disappearance, bands of color usually shrink away at one end (p. 184). (e) The ends of a series of spots are more

variable than the middle. This is only a special case of Bateson's ('94) law (p. 185). (f) The position of spots situated near the outer edges of the wing is largely controlled by the wing-folds or creases (p. 185).

(9) The scales in Lepidoptera do not strengthen the wings or aid the insects in flight. The vast majority of the scales are merely color-bearing organs, which have been developed under the influence of Natural Selection. The phylogenetic appearance and development of scales upon the originally scaleless ancestors of the Lepidoptera did not alter the *efficiency* of their wings as *organs of flight.* It is probable, therefore, that this efficiency was an optimum before the scales appeared (p. 197).

(10) A systematic study of the Danaoid Heliconidae demonstrates that their color-patterns can be placed in two types. Type 1, the more complex, is closely related to the coloration of the Danaidae from which the Danaoid Heliconidae sprang, and is therefore, phylogenetically speaking, the older type of coloration. This type is characteristic of the genera Lycorea, Melinaea, and Mechanitis, and I have called it the "Melinaea" type. It is characterized by the fact that the wings are rufous and black in color, and crossed by a definite system of yellow bands. Type 2, the "Ithomia" type, is characteristic of the genera Ithomia, Ituna, and Thyridia. The "Ithomia" type has been derived from the "Melinaea" by the originally rufous and yellow areas upon the wings having become transparent (p. 204).

(11) The phylogenetic origin of the "Melinaea" and "Ithomia" types of coloration can be accounted for upon the supposition, that when the species of the Danaoid Heliconidae began to segregate out from the Danaidae they were for a time rare (p. 215).

(12) A record of the characteristic markings upon the wings of the Danaoid and Acraeoid Heliconidae shows that, physiologically speaking, the colors red, rufous, yellow, and white are closely related, and that black is quite distinct from these, being the least variable color of all (p. 220).

(13) In both the Danaoid and Acraeoid Heliconidae, whatever color-variation affects that part of the *fore* wing which is adjacent to the body of the insect, almost always the same color-variation affects the homologous area of the *hind* wing in a similar manner (p. 218, and Fig. 99).

(14) The smaller yellow spots upon the wings of the Heliconi-

dae are more liable to color-variations than are the larger ones. This is what we should expect, if the theory of mimicry be true; for large spots are more conspicuous, and therefore their preservation is more important (p. 220). This rule, however, does not hold for the black markings of the wing (p. 222).

(15) The mathematical chance against five similar and independent color-sports arising in the genus Melinaea is as 2,830,000 to 1. Hence, the five Melinaeas which display the "inner black" as a double spot are probably descended from a single ancestor (p. 219).

(16) The marginal spots of the fore wing in the Danaoid Heliconidae show a marked tendency to appear either as 2 or 3, or else as 6 or 7 spots (p. 223, Fig. 101). The marginal spots of the *hind* wing show a marked tendency to appear either as 4 or 5 spots (p. 223, and Fig. 102).

(17) The 200 species of Papilio in South America display 36 distinct colors, while the 450 species of Danaoid Heliconidae exhibit only 15. Hence the numbers of the *species* and of the *colors* are almost in inverse ratio in the two groups. This may be explained by the fact, that the Danaoid Heliconidae mimic one another, while the Papilios do not (p. 224).

(18) The colors are dull upon those portions of the hind wing which are hidden from view by the overlapping fore wing (p. 225).

(19) There is no lack of individual variability among the species of the Danaoid Heliconidae; yet the species as a whole vary but little from the two great types of color-pattern represented by Melinaea and Ithomia. In order to account for this remarkable fact I am forced to resort to Fritz Müller's theory of mimicry (p. 225).

TABLE 1.

Showing the Variations in Color of the "Inner Rufous" (Area I in Figures on Plate **4**) of the *fore wing* in the Danaoid Heliconidae.

GENERA.	Rufous.	Translucent rufous.	Translucent, slightly rufous.	Transparent.	Transparent, slightly yellow.	Translucent yellow.	Yellow.	Black.	White.
Lycorea	5								
Ituna				2				1	
Athesis			2	1					
Thyridia				5					
Athyrtis	2								
Olyras	1		1	1				1	
Eutresis		2							
Aprotopos			1					1	
Dircenna	1	3		4	2	1		1	
Callithomia	1							2	
Epithomia	1	1							
Ceratinia	28	1	2	7	1			2	
Sais	5								
Scada						7			
Mechanitis	18				1		1	4	
Napeogenes	7	3	2	12		3		3	
Ithomia	29	13	15	120	26	5		3	1
Aeria						4			
Melinaea	22					2			
Tithorea	4							6	
Total	124	23	23	152	30	22	1	24	1
Excluding Ithomia	95	10	8	32	4	17	1	21	0

Note: The costal edge of the fore wing is usually black; it is rufous or brown, however, in 47 Ithomias and dull yellow in one; it is rufous in two species of Sais, in one species of Ceratinia, and in one species of Athesis. Hence it is black in 348 species and light colored in 52.

TABLE 2.

Showing the Variation (presence or absence) of the "Inner Black" (Area II) of the *fore wing* in the Danaoid Heliconidae.

GENERA.	Present.	Absent.	Remarks.
Lycorea	5		
Ituna	3		
Athesis	2	1	
Thyridia	5		
Athyrtis	2		
Olyras	4		
Eutresis	2		
Aprotopos	2		
Dircenna	8	4	
Callithomia	3		
Epithomia	2		
Ceratinia	29	12	
Sais	4	1	
Scada		7	
Mechanitis	23	1	
Napeogenes	13	17	Appears as 2 spots in 1 species.
Ithomia	72	140	Appears as 2 spots in 1 species.
Aeria		4	
Melinaea	21	3	Appears as 2 spots in 5 species.
Tithorea	10		
Total	210	190	
Excluding Ithomia .	138	50	

TABLE 3.

Showing the Variations in Color of the "Inner Yellow" (Area III) of the *fore wing* in the Danaoid Heliconidae.

GENERA.	Rufous.	Translucent rufous.	Translucent, slightly rufous.	Transparent.	Translucent, slightly yellow.	Translucent yellow.	Yellow.	Black.	White, generally translucent.
Lycorea							5		
Ituna				3					
Athesis			2	1					
Thyridia				5					
Athyrtis	1						1		
Olyras						4			
Eutresis			1	1					
Aprotopos					1		1		
Dircenna		1	2	3	6				
Callithomia							3		
Epithomia						1	1		
Ceratinia	16	1	1	7	7	2	6	1	
Sais	2						2	1	
Scada						7			
Mechanitis	11						13		
Napeogenes	2		4	14	1	4	5		
Ithomia	10	11	14	124	23	9	13	1	7
Aeria							4		
Melinaea	14					4	4		2
Tithorea							6	3	1
Total	56	13	24	158	38	31	64	6	10
Excluding Ithomia .	46	2	10	34	15	22	51	5	3

TABLE 4.

Showing the presence or absence of the "Middle Black" Mark (Area IV) of the *fore wing* in the Danaoid Heliconidae.

GENERA.	Present.	Absent.	Present, but changed to some color other than black.
Lycorea	5		
Ituna	3		
Athesis	3		
Thyridia	5		
Athyrtis	2		
Olyras	2		
Eutresis	2		
Aprotopos	2		
Dircenna	11	1	
Callithomia	3		
Epithomia	2		
Ceratinia	34	7	
Sais	5		
Scada	7		
Mechanitis	24		
Napeogenes	25	5	
Ithomia	194	6	12 rufous or brown.
Aeria	4		
Melinaea	23	1	
Tithorea	10		
Total	366	20	12
Excluding Ithomia .	172	14	

TABLE 5.

Showing the Variation in Color of the "Middle Yellow" Band (Area V) of the *fore wing* in the Danaoid Heliconidae.

GENERA.	Rufous.	Translucent rufous.	Translucent, slightly rufous.	Transparent.	Translucent, slightly yellow.	Translucent yellow.	Yellow.	Black.	White, more or less translucent.
Lycorea							5		
Ituna				3					
Athesis			2	1					
Thyridia				5					
Athyrtis	1						1		
Olyras				1		3			
Eutresis				2					
Aprotopos				1			1		
Dircenna			2	3	2	2	3		
Callithomia							3		
Epithomia						1	1		
Ceratinia			2	6	4	5	24		
Sais							5		
Scada						6		1	
Mechanitis	4				1		19		
Napeogenes	2		3	11	4	4	6		
Ithomia	5	6	12	123	24	8	14		20
Aeria							4		
Melinaea	2			3		2	15		2
Tithorea							7	1	2
Total	14	6	21	159	35	31	108	2	24
Excluding Ithomia	9	0	9	36	11	23	94	2	4

TABLE 6.

Showing approximately the Number of Species in which the "Outer Yellow" (Area VI) of the *fore wing* in the Danaoid Heliconidae appears as a separated Marking. It is usually fused with the "Middle Yellow" Area.

GENERA.	Wholly fused with middle yellow.	Partially fused with middle yellow.	Separate.	Absent.
Lycorea		1	4	
Ituna	2	1		
Athesis	3			
Thyridia	5			
Athyrtis			2	
Olyras	1	3		
Eutresis		2		
Aprotopos		2		
Dircenna	7 ?	5 ?		
Callithomia		1	2	
Epithomia		1	1	
Ceratinia	22	16 about	3 about	
Sais			2	3
Scada			4	3
Mechanitis		1	20	3
Napeogenes	6		24 about	
Ithomia	200 about			
Aeria	4			
Melinaea	1		17	6
Tithorea			10	
Total	about 250	about 30	about 90	perhaps 20

TABLE 7.

Showing the Degree of Development of the "Outer Black" (Area VII) of the *fore wing* in the Danaoid Heliconidae.

Genera.	Well developed over a large area of the fore wing.	Reduced to the outer margin of the fore wing.	Present, but changed to another color.
Lycorea	5		
Ituna		3	
Athesis	2	1	
Thyridia		5	
Athyrtis	2		
Olyras	3	1	
Eutresis	2		
Aprotopos	1	1	
Dircenna	5	7	
Callithomia	3		
Epithomia	2		
Ceratinia	28	13	2 partly rufous.
Sais	2		3 partly rufous.
Scada	3	4	
Mechanitis	22	2	
Napeogenes	26	4	
Ithomia	161	54	16 rufous or brown.
Aeria	4		
Melinaea	24		1 partly rufous.
Tithorea	10		
Total	305	95	22 partly rufous.

TABLE 8.

Showing the presence or absence of the "Longitudinal Black Stripe" (Area VIII) which runs parallel with the lower Edge of the *fore wing* in the Danaoid Heliconidae.

GENERA.	Present and well developed as a stripe.	Much reduced.	Absent.	Whole area suffused with black.
Lycorea	5			
Ituna	3			
Athesis	3			
Thyridia	5			
Athyrtis	2			
Olyras	3			1
Eutresis	2			
Aprotopos	1			1
Dircenna	7	3		2
Callithomia			1	2
Epithomia.	1	1		
Ceratinia	37	2		2
Sais	3	1	1	
Scada	6		1	
Mechanitis	17		2	5
Napeogenes	20	6		4
Ithomia	200	6	4	2
Aeria	4			
Melinaea	14	5	5	
Tithorea	5			5
Total	338	24	14	24

TABLE 9.

Showing the Manner of Occurrence of the Marginal Spots (Area IX) of the *fore wing* in the Danaoid Heliconidae.

GENERA.	Without spots	1 spot.	2 spots.	3 spots.	4 spots.	5 spots.	6 spots.	7 spots.	8 spots.	9 spots.
Lycorea . . .	5									
Ituna	3									
Athesis . . .	3									
Thyridia . . .	4			1						
Athyrtis . . .	1							1		
Olyras . . .	3						1			
Eutresis . . .	2									
Aprotopos . .	1	1								
Dircenna . . .	11		1							
Callithomia . .	1				2					
Epithomia . .	2									
Ceratinia . .	19	1	3	1			4	12	1	
Sais	5									
Scada	4			1		1		1		
Mechanitis . .	17		1		2		1	3		
Napeogenes . .	14		1	3	1		5	3	3	
Ithomia . . .	137	2	14	14	7	16	14	8		
Aeria	4									
Melinaea . . .	13		1			2	4	3	1	
Tithorea . . .	5		1		1			2		1
Total	254	4	22	20	13	19	29	33	5	1

TABLE 10.

Showing the Color-Variations affecting the "Inner Rufous" (Area X) of the *hind wing* in the Danaoid Heliconidae.

GENERA.	Rufous.	Translucent rufous.	Translucent, slightly rufous.	Transparent.	Translucent, slightly yellow.	Translucent yellow.	Yellow.	Black.
Lycorea . . .	5							
Ituna		1		2				
Athesis			2	1				
Thyridia . . .				4	1			
Athyrtis . . .	2							
Olyras	3					1		
Eutresis . . .		2						
Aprotopos . . .	1			1				
Dircenna . . .			8	2	2			
Callithomia . .	3							
Epithomia . . .	2							
Ceratinia . . .	23		3	6	6	1	2	
Sais	5							
Scada						7		
Mechanitis . .	16						4	4
Napeogenes . .	7	6		6	6	5		
Ithomia . . .	31	14	12	133	14	5	1	2
Aeria							4	
Melinaea . . .	19					4	1	
Tithorea . . .	6							4
Total	123	23	25	155	29	23	12	10

TABLE 11.

Showing the Variations of the "Middle Black Stripe" (Area XI) of the *hind wing* in the Danaoid Heliconidae.

GENERA.	Present.	Absent.	Fused with the marginal black.	Changed color.
Lycorea	5			
Ituna	2	1		
Athesis	2	1		
Thyridia	2	2	1 partially	
Athyrtis	2			
Olyras	1	2		1 changed to translucent yellow ?
Eutresis		2		
Aprotopos	2			
Dircenna	4	7	1	
Callithomia			3	
Epithomia		2		
Ceratinia	21		20	
Sais		1	4	
Scada		7		
Mechanitis	22	2		
Napeogenes	15		15	
Ithomia	45	1	168	
Aeria		4		
Melinaea	15	9		
Tithorea	8	2		
Total	146	43	212	1 ?

TABLE 12.

Showing the Color-Variations of the "Outer Rufous" (Area XII) of the *hind wing* in the Danaoid Heliconidae.

GENERA.	Rufous.	Translucent rufous.	Translucent, but slightly rufous.	Transparent.	Translucent, but slightly yellow.	Translucent yellow.	Yellow.	Black.	White, somewhat translucent.
Lycorea	5								
Ituna		1		2					
Athesis			2	1					
Thyridia				4	1				
Athyrtis	2								
Olyras	3					1			
Eutresis	1	1							
Aprotopos	1			1					
Dircenna	2	4	3	3					
Callithomia	1							2	
Epithomia	2								
Ceratinia	29	1	1	7	1			2	
Sais	5								
Scada						7			
Mechanitis	21							3	
Napeogenes	15							15	
Ithomia	44			2	1			165	
Aeria								4	
Melinaea	17						1	6	
Tithorea	5						2	2	1
Total	153	7	6	20	3	8	3	199	1
Excluding Ithomia	109	7	6	18	2	8	3	34	1

TABLE 13.

Showing the presence or absence, and Color-Changes of the "Outer Black" (Area XIII) of the *hind wing* in the Danaoid Heliconidae.

GENERA.	Present.	Absent.	Changed color.
Lycorea	5		
Ituna	3		
Athesis	3		
Thyridia	5		
Athyrtis	2		
Olyras	4		
Eutresis	2		
Aprotopos	2		
Dircenna	12		
Callithomia	3		
Epithomia	2		
Ceratinia	41		
Sais	5		
Scada	7		
Mechanitis	24		
Napeogenes	30		
Ithomia	210	1	11 changed to rufous or brown.
Aeria	4		
Melinaea	24		
Tithorea	10		
Total	398	1	11

TABLE 14.

Showing the Number of the Marginal Spots of the *hind wing* in the Danaoid Heliconidae.

GENERA.	Without spots.	1 spot.	2 spots.	3 spots.	4 spots.	5 spots.	6 spots.	7 spots.	8 spots.	9 spots.
Lycorea . . .		1					3	1		
Ituna	2	1								
Athesis . . .				1	1		1			
Thyridia . . .	4	1								
Athyrtis . . .	1									1
Olyras	3		1							
Eutresis . . .	1						1			
Aprotopos . .				2						
Dircenna . . .	10		1						1	
Callithomia . .	2		1							
Epithomia . .	1					1				
Ceratinia . . .	18	3	1	2	5	5	2	4	1	
Sais	4				1					
Scada	3				1	1	2			
Mechanitis . .	18		1	1	2	2				
Napeogenes . .	21		1	1	1	5		1		
Ithomia . . .	164		8	6	12	9	6	6	1	
Aeria	4									
Melinaea . . .	19				1			3	1	
Tithorea . . .	4				2	2	2			
Total	279	6	14	13	26	25	17	15	4	1

TABLE 15.

Showing the Color-Variations of the "Inner Rufous" Area of the *fore wing* in Heliconius and Eueides.

	Rufous.	Reddish rufous.	Yellow.	Ocher.	White.	Black.	Irides-cent blue.
Heliconius . .	35	8	11		2	29	26
Eueides . . .	14			1		3	
Total . . .	49	8	11	1	2	32	26

Note: The costal edge of the fore wing is always black.

TABLE 16.

Showing the Variations affecting the "Inner Black" Area of the *fore wing* in Heliconius and Eueides.

	Black.	Iridescent blue.	Rufous.
Heliconius	85	26	
Eueides	13		5
Total	98	26	5

Note: In 54 species of Heliconius the inner rufous is entirely suffused with black.

TABLE 17.

Showing the Color-Variations of the "Inner Yellow" Area of the *fore wing* in Heliconius and Eueides.

	Rufous.	Red.	Yellow.	Ocher.	White.	Black.	Irides-cent blue.
Heliconius . .	11	12	54		20	12	3
Eueides . . .	6			12			
Total . . .	17	12	54	12	20	12	3

TABLE 18.

The "Middle Black" Area in the *fore wing* in Heliconius is present as a Black or Blue Marking in 99 Species and absent in 12. It is present as a Black Mark in all 18 Species of Eueides.

TABLE 19.

Showing the Color-Variation of the "Middle Yellow" Area of the *fore wing* in Heliconius and Eueides.

	Rufous.	Reddish rufous.	Yellow.	Ocher.	White.	Black.
Heliconius .	11	12	65		23	
Eueides . .	5			12	1	
Total . . .	16	12	65	12	24	

TABLE 20.

Showing the Color-Variations of the "Outer Yellow" Area of the *fore wing* in Heliconius and Eueides.

	Rufous.	Reddish rufous.	Yellow.	Ocher.	White.	Black.	Irides-cent blue.
Heliconius . .	2	1	47		24	33	4
Eueides . . .				6	1	11	
Total	2	1	47	6	25	44	4

TABLE 21.

The "Outer Black" Area of the *fore wing* in all the 111 species of Heliconius known to me is Black or Iridescent Blue. It is Black in all 18 Eueides.

TABLE 22.

Showing the Manner of Occurrence of the Marginal Spots of the *fore wing* in Heliconius and Eueides.

	Without spots.	1 spot.	2 spots.	3 spots.	4 spots.	5 spots.	6 spots.	7 spots.	8 spots.	9 spots.
Heliconius . .	89		5	2	5	3	4	2		1
Eueides . . .	14		3				1			
Total	103		8	2	5	3	5	2		1

TABLE 23.

Showing the Variations affecting the "Longitudinal Black Stripe" of the *fore wing* in Heliconius and Eueides.

	Whole area suffused with black.	Well developed as a black stripe.	Absent (area suffused with rufous).
Heliconius	75	23	13
Eueides	2	16	
Total	77	39	13

TABLE 24.

Showing the Color-Variations of the "Inner Rufous" Area of the *hind wing* in Heliconius and Eueides.

	Rufous.	Reddish rufous.	Yellow.	Ocher.	Iridescent green.	Black.	Iridescent blue.	Black and yellow.	Black and rufous.	Black and reddish rufous.
Heliconius . .	42	7	3		1	16	26	10	1	5
Eueides . . .	15			2		1				
Total	57	7	3	2	1	17	26	10	1	5

TABLE 25.

Showing the Variations of the "Middle Black Stripe" of the *hind wing* in Heliconius and Eueides.

	Well developed as a more or less distinct stripe.	Absent (suffused with black).	Absent (place taken by red or rufous).	Absent (place taken by ocher color).
Heliconius	47	59	5	
Eueides	6		10	1
Total	53	59	15	1

TABLE 26.

Showing the Color-Variations of the "Outer Rufous" Area of the *hind wing* in Heliconius and Eueides.

	Rufous.	Reddish rufous.	Yellow.	White.	Ocher.	Black.	Iridescent blue.
Heliconius . .	30	4	19	3		49	6
Eueides . . .	17					1	
Total	47	4	19	3		50	6

TABLE 27.

The "Outer Black" Area of the *hind wing* is Black in 106 species of Heliconius, White in 4, and Yellow in 1. It is Black in all the 18 species of Eueides known to me.

TABLE 28.

Showing the Number of Species in each Genus of the Heliconidae examined, and also the Number known according to the Enumeration of Staudinger ('84–'88).

GENERA.	Number of species examined by me.	Number of species known to Staudinger ('84–'88).
Lycorea	4 species and 1 var.	4 species and 1 var.
Ituna	3	4
Athesis	3	4
Thyridia	5	4
Athyrtis	2	2
Olyras	4	5
Eutresis	2	2
Aprotopos	2	4
Dircenna	12	20+
Callithomia	3	8
Epithomia	2	2
Ceratinia	41	50+
Sais	5	4
Scada	7	9
Mechanitis	10 species, 14 var.	10 species, 13 var.
Napeogenes	30	30+
Ithomia	212	230+
Aeria	4	4
Melinaea	24	25
Tithorea	10	18
Total of Danaoid Heliconidae.	400	453+
Heliconius	111	130
Eueides	18	24
Total	529	607+

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TABLE OF CONTENTS.

PART A.

GENERAL PHENOMENA OF COLOR IN LEPIDOPTERA.

I. CLASSIFICATION OF COLORS.

PAGE
(1) Pigmental Colors 169
(2) Structural Colors 170
(3) Combination Colors 171
(4) Quantitative Determination of Pigmental Colors 172
(5) Spectrum Analysis of Colors of Lepidoptera 173
(6) Summary of Results 174

II. THE ESSENTIAL NATURE OF PIGMENTAL COLOR IN LEPIDOPTERA.

(1) Pigments of Larvae 174
(2) Pigments of Imagines 175

III. DEVELOPMENT OF THE VARIOUS COLORS IN THE PUPAL WINGS.

(1) Historical Account of previous Researches 176
(2) Development of Color in the Pupal Wings of Callosamia promethea 178
(3) Development of Color in the Pupal Wings of Danais plexippus (archippus) 180

IV. THE LAWS WHICH GOVERN THE COLOR-PATTERNS OF BUTTERFLIES AND MOTHS.

(1) Historical Account of previous Researches 181
(2) Laws of Color-Patterns 183
(3) Detailed Discussion of the Laws of Color-Patterns 185
(4) Origin of Color-Variations 189
Bibliography of Color-Aberrations 190
(5) Climate and Melanism 190
(6) Relation between Climate and Colors of Papilios 191

V. THE CAUSES WHICH HAVE LED TO THE DEVELOPMENT AND PRESERVATION OF THE SCALES OF THE LEPIDOPTERA.

(1) Experiments and Theory 192
(2) Summary of Conclusions 197

PART B.

COLOR-VARIATIONS IN THE HELICONIDAE.

I. GENERAL CAUSES WHICH DETERMINE COLORATION IN THE HELICONIDAE.

II. METHODS PURSUED IN STUDYING THE COLOR-PATTERNS OF THE HELICONIDAE.

(1) The Two Types of Coloration in the Danaoid Heliconidae 204
(2) Detailed Description of the Melinaea Type of Coloration 205

III. General Discussion of the Color-Patterns and of Mimicry in the Genera Heliconius and Eueides.

(1) The Four Color-Types in the Genus Heliconius . . . 208
(2) Mimicry between the genus Heliconius and the Danaoid Group 209
(3) The Three Color-Types in the Genus Eueides . . . 210
(4) Detailed Discussion of Plates 5–8 210

IV. General Discussion of the Color-Patterns and of Mimicry among the Danaoid Heliconidae.

(1) The Origin of the two Types of Coloration . . . 214
(2) Mimicry among the Danaoid Heliconidae 216

V. Quantitative Determination of the Variations of the characteristic Wing-Markings in the Acraeoid and Danaoid Heliconidae.

(1) Variations of the "Inner Rufous" Areas of the Fore and Hind Wings 217
(2) The "Inner Black" Spot 218
(3) Variations of the "Inner Yellow" and "Middle Yellow" Areas 219
(4) Variations of the "Middle Black" Mark of the Fore Wing 221
(5) Variations of the "Outer Yellow" Area of the Fore Wing 221
(6) The Relative Permanency of the Black Areas upon the Fore and Hind Wings 222
(7) The "Middle Black Stripe" of the Hind Wing . . 222
(8) Variations of the Marginal Spots of the Fore Wing . . 223
(9) The Marginal Spots of the Hind Wing 223

VI. Comparison of the Color-Variations of the Papilios of South America with those of the Heliconidae.

PART C.

General Summary of Results believed to be new to Science.

Tables 230
Bibliography 249
Explanation of Plates . . . .

PLATE I.

ABBREVIATIONS.

B. Back surface covered with wings.
O. Orifice for admission of light.
F. Front surface covered with wings.
S. Spectroscope.

Arrow indicates directions of rays of light.

Fig. 1. Perspective view of spectroscopic apparatus used in determining the composition of the colors of Lepidoptera.

Fig. 2. Horizontal section of same. See p. 175.

Fig. 3. Pendulum used in determination of the frictional resistance between the air and the wings of Lepidoptera. See p. 193.

Figs. 4, 5. Diagrams to illustrate Keeler's method of projection, as applied to Lepidoptera. See p. 207.

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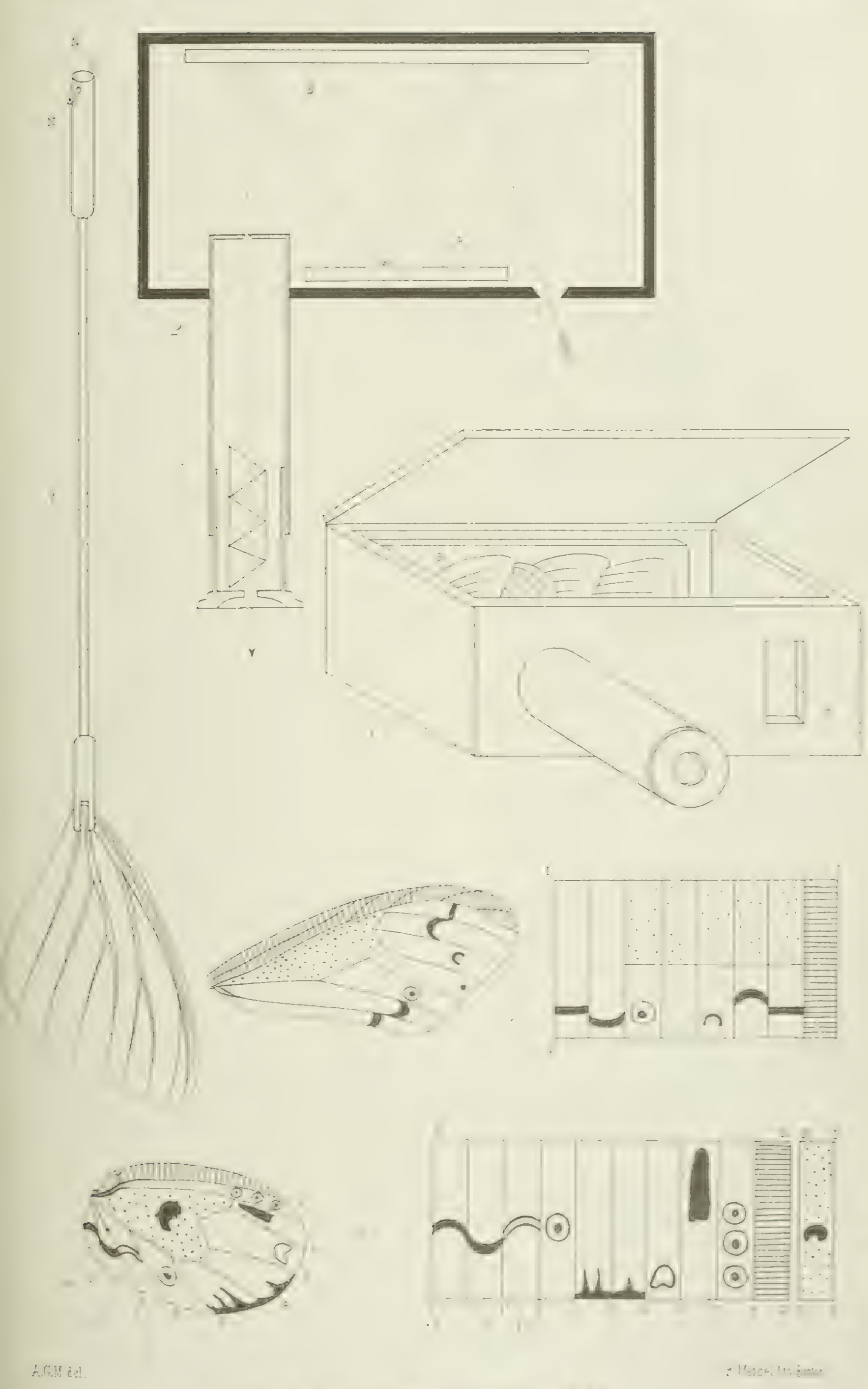

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PLATE 2.

Diagrams to illustrate the laws which govern the Color-Patterns of Lepidoptera.

Fig. 6. Euthalia bellata (W. L. Distant, '82–'86, Plate 43, Fig. 12). Illustrates the law of bilaterality of spots. See p. 183.

Fig. 7. Zethera musa (G. Semper, '86–'92, Taf. 7, Fig. 10). Bilaterality of double spots. See p. 183.

Fig. 8. Eye-spots in Morpho. See p. 182, 183.

Fig. 9. Parthenos gambrisius (W. L. Distant, '82–'86, Plate 11, Fig. 7). A series of complex spots, each one being similar to the rest, and bilaterally symmetrical.

Figs. 10, 11. Ornithoptera urvillana and O. priamus (R. H. F. Ripon, '89–'93). Spots within spots, all being bilaterally symmetrical.

Figs. 12, 13. Hestia jasonia and H. leuconoe. Axis of lateral symmetry (H, H), for spots passes through center of interspace. H. jasonia (F. Moore, '90–'96, Plate 3, Fig. 1). H. leuconoe (G. Semper, '86–'92, Taf. 1, Fig. 3).

Fig. 14. Papilio emalthion, to illustrate fusion of two rows of spots.

Fig. 15. Ornithoptera trojana, an apparent exception to the law of bilaterality. See p. 187.

Fig. 16. Limenitis proserpina (S. H. Scudder, '88–'89, Plate 2, Fig. 9), showing fusion of two rows of differently colored spots. See p. 187.

Fig. 17. Saturnia spini, false eye-spot. See p. 187.

Fig. 18. Cases of degeneration of bands of color. See p. 184.

Fig. 19. Missanga patina (F. Moore, '90–'96, Plate 72, Fig. 2^{c}). Exceptional form of eye-spot. See foot note p. 186.

Figs. 20–23. Hypothetical conditions of coloration, not found in nature, being contrary to the laws of color-pattern. See p. 188.

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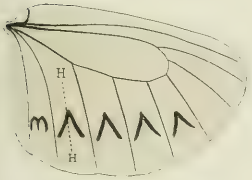

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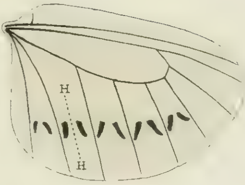

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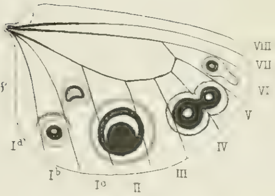
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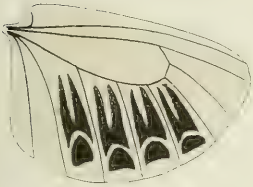

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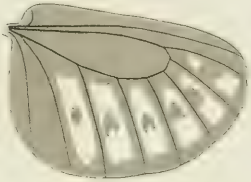

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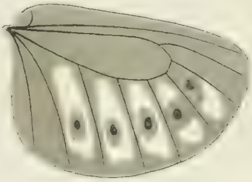

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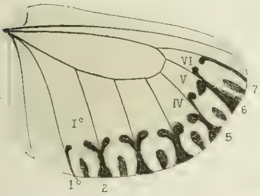
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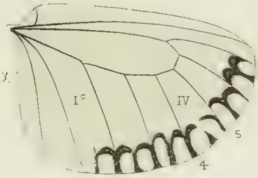

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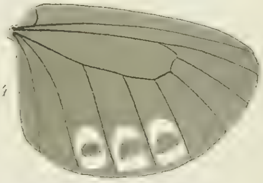

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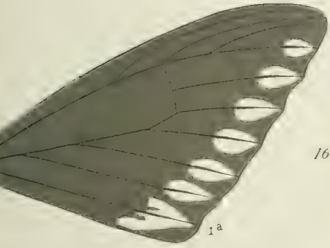

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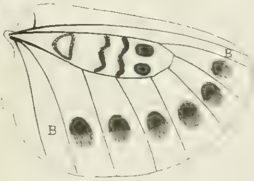

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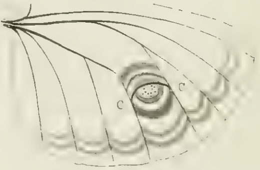

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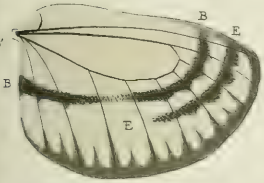

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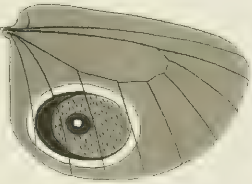

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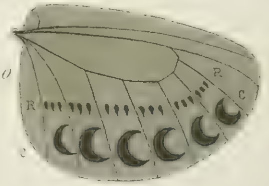

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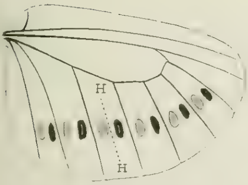

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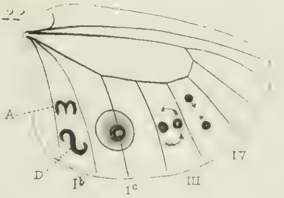
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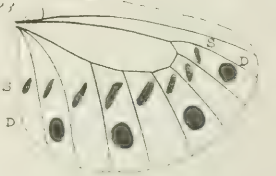

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B. Meisel lith. Boston

PLATE 3.

To illustrate color-development in Callosamia promethea and Danais plexippus.

Fig. 24. Enlarged view of pupal wing of C. promethea in the "white stage." See p. 178.

Fig. 25. Scale from wing of C. promethea in white stage of color-development, showing the total absence of pigment in the scale. See p. 178.

Fig. 26. Scale from light drab-colored area of mature wing of C. promethea.

Figs. 27, 36, and 33. Successive stages in the formation of color in pupal hind wing of C. promethea.

Figs. 28, 37–40. Successive stages in the formation of color in the pupal fore wing of ♀ C. promethea. See p. 179, 180.

Figs. 29, 30–35. Successive stages in the formation of color in the pupal wings of ♂ C. promethea. (Figs. 29, 30–33, 35 fore wing; Fig. 34 hind wing.) See p. 179, 180.

Figs. 34 and 41. Pupal hind wings of C. promethea, respectively mature ♂ and ♀.

Figs. 42–45. Successive stages in the color-development of D. plexippus. See p. 180–181.

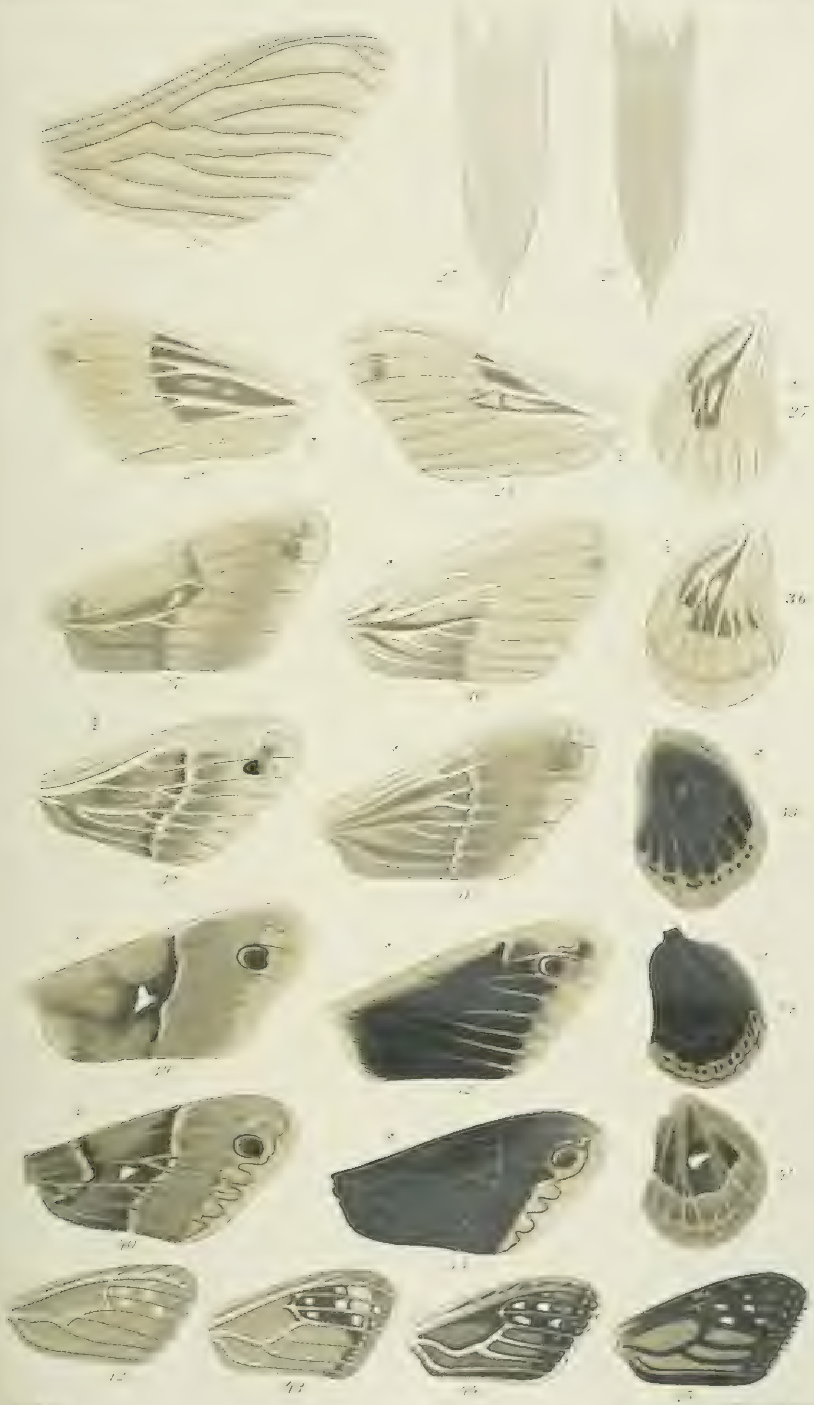

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PLATE 4.

Systematic analysis of the characteristic markings upon the wings of the Heliconidae. Homologous markings are designated by the same numerals, I, II, III, etc.

Fig. 46. Lycorea ceres; an example of the "Melinaea type" of coloration. See p. 205.

Fig. 47. Thyridia psidii; an example of the "Ithomia type" of coloration. See p. 206 and Plate **7**, Fig. 79.

Fig. 48. Melinaea paraiya.

Fig. 49. Ceratinia ninonia.

Fig. 50. Heliconius antiochus.

Fig. 51. Napeogenes duessa.

Fig. 52. Ithomia sao.

Fig. 53. Melinaea gazoria.

Fig. 54. Ithomia nise.

Fig. 55. Mechanitis polymnia.

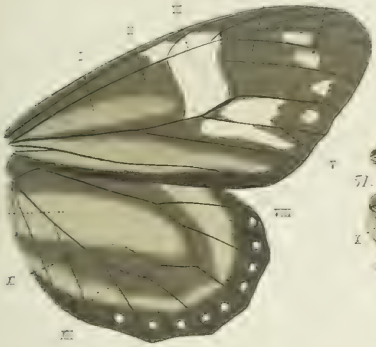
Fig. 56. Eueides cleobaea.

Fig. 57. Tithorea furia var.

Fig. 58. Heliconius eucrate.

Fig. 59. Heliconius melpomene.

Fig. 60. Heliconius erato.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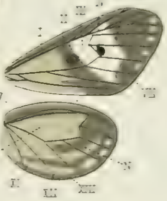
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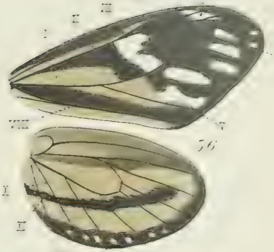
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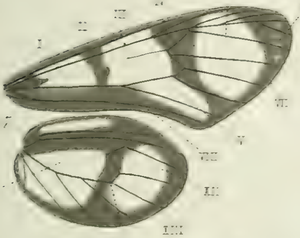
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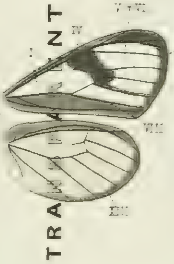
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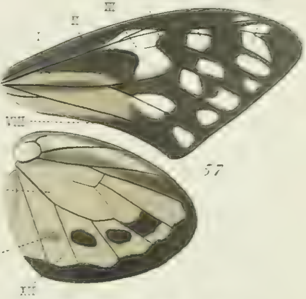
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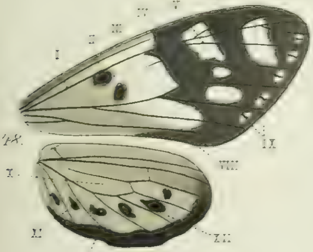
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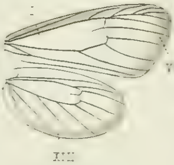
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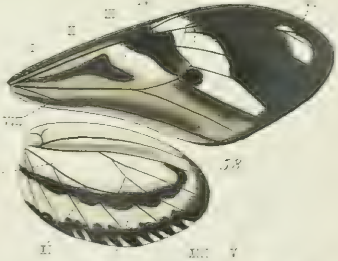
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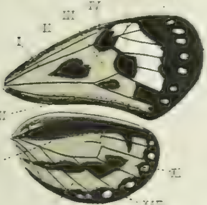
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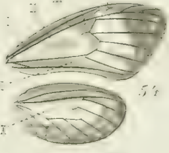
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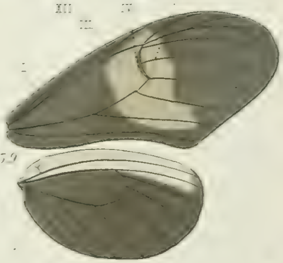
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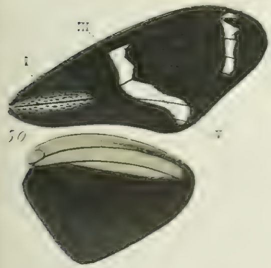
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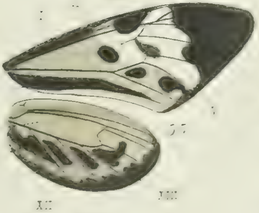
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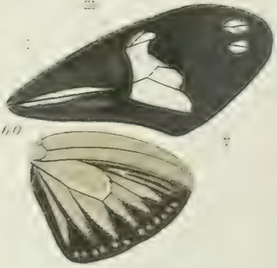
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PLATE 5.

Color-patterns of the Antiochus and Erato groups of the Heliconidae projected by Keeler's method. See p. 207.

Figs. 61, 62. Heliconius sara and H. antiochus, to show variation of yellow to white. See p. 210, and Fig. 50, Plate **4**.

Fig. 63. H. galanthus, showing development of white.

Fig. 64. H. charitonia, rows of double spots.

Fig. 65. H. phyllis, close relation between yellow and red.

Fig. 66. H. ricini.

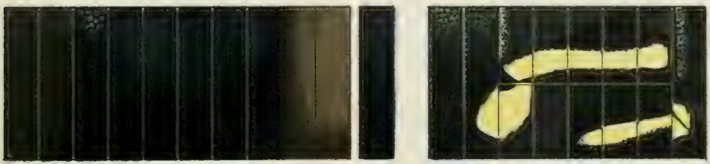
Figs. 67, 68. H. erato: two color-types.

Fig. 69. H. claudia; an example of the Sylvanus group.

HIND WING

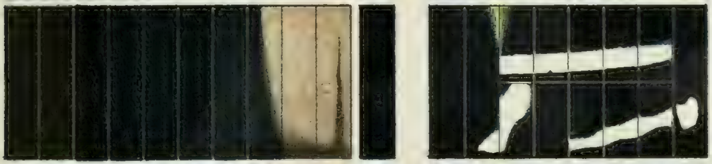
FORE WING

61.



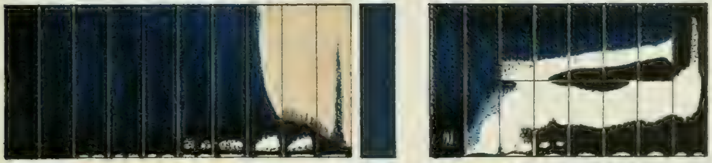
Heliconius sara Godt.

62.



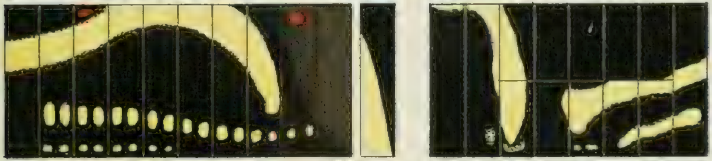
H. antiochus Linn.

63.



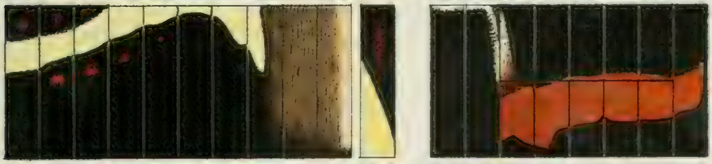
H. galanthus Bates.

64.



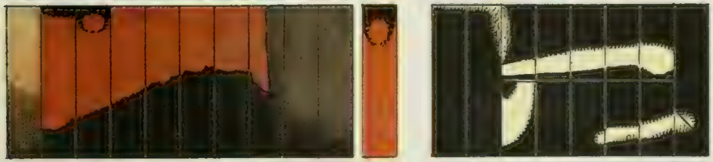
H. charithonia Linn.

65.



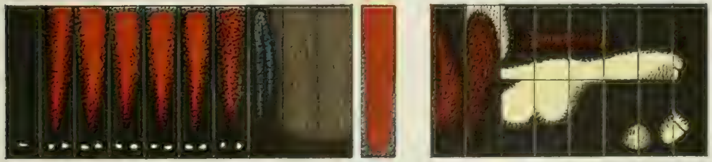
H. phyllis Fabr.

66.



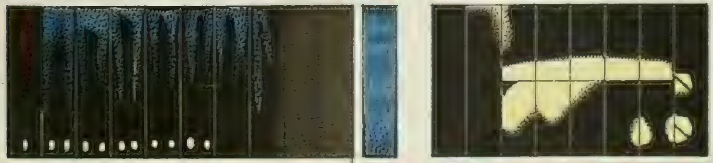
H. ricini Linn.

67.



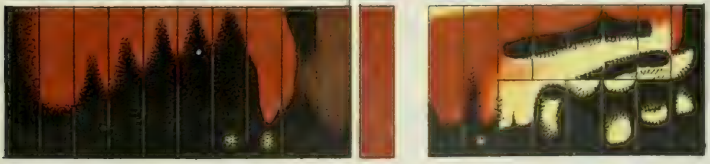
H. erato Linn.

68.



H. erato Linn.

69.



H. claudia Godm. & Salv.

A. G. M. del.

B. Meisel lith. Boston.

PLATE 6.

Color-patterns of the Melpomene group of Heliconius and of the genus Eueides.

Fig. 70. H. melpomene, the type of the Melpomene group. See p. 212, and Fig. 59, Plate **4**.

Fig. 71. H. melpomene var. callicopis, showing the breaking up of the red area of the primaries.

Fig. 72. H. melpomene var. cybele; the fore wing has assumed a color-pattern which recalls the "Melinaea type" of coloration found in the Danaoid Heliconidae.

Fig. 73. H. thelxiope, derived phylogenetically from H. melpomene, and showing a rather close approach to the "Melinaea type" of coloration. See p. 212.

Fig. 74. H. vesta.

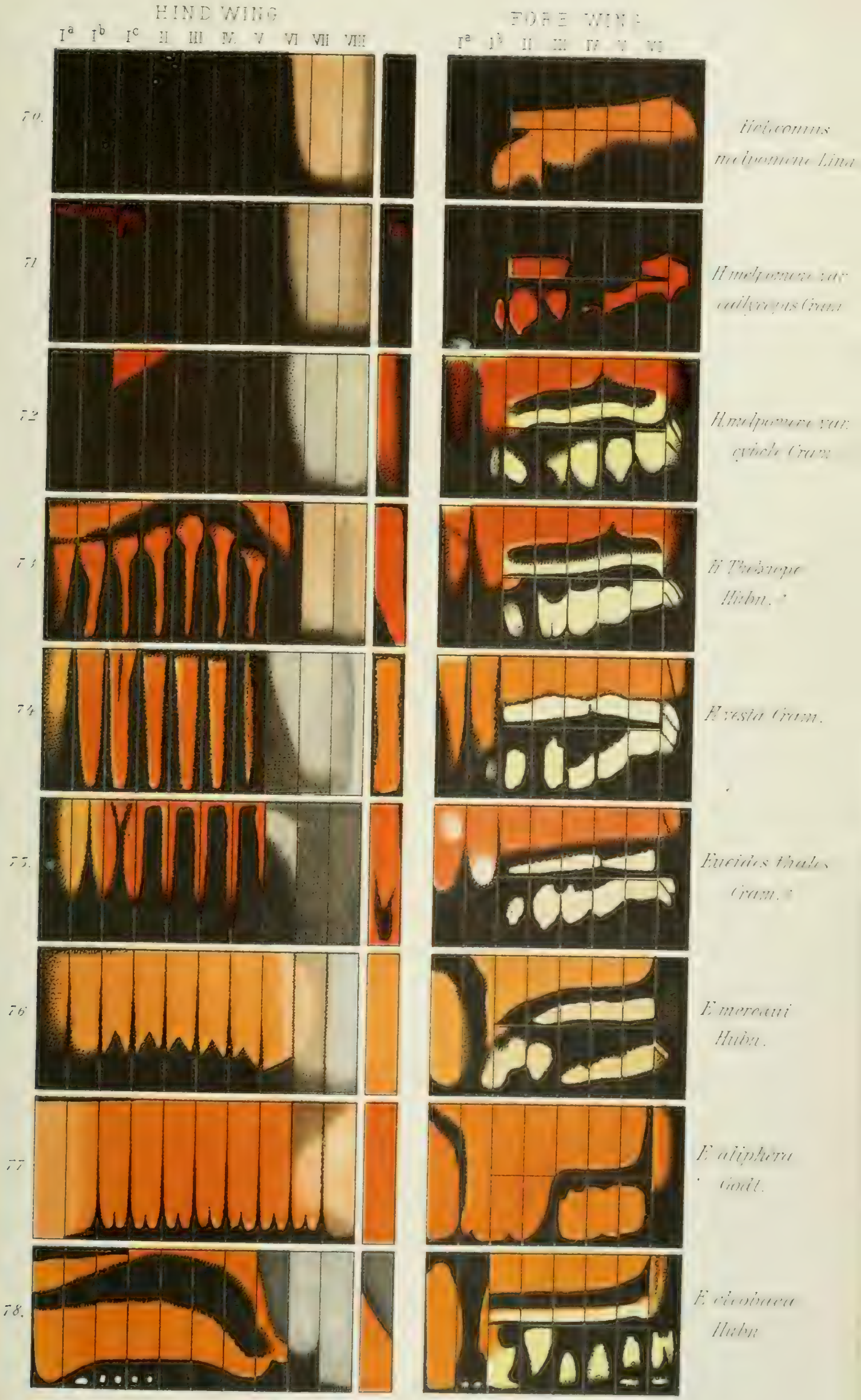
Fig. 75. Eueides thales ♂; represented to show the close resemblance of its color-pattern to H. vesta. See p. 212.

Figs. 76, 77. E. mereaui and E. aliphera. E. mereaui is intermediate in color-pattern between E. thales and E. aliphera.

Fig. 78. Eueides cleobaea, to show the close approach of this insect to the "Melinaea type" of coloration.

MAYER - COLOR AND COLOR PATTERNS

PLATE. 6.


HIND WING
Iª Iᵇ Iᶜ II III IV. V VI VII VIII
FORE WING
Iª Iᵇ II III IV V VI
70.
71
72
73
74
75.
76
77
78.
Heliconius melpomene Linn.
H. melpomene var. callycopis Cram.
H. melpomene var. cybele Cram.
H. Thelxiope Hübn.
H. vesta Cram.
Eueides thales Cram.
E. mereaui Hübn.
E. aliphera Godt.
E. cleobaea Hübn.

A. G. M. del.

PLATE 7.

Intended to show some types of coloration which are found in the Danaoid Heliconidae, and also the remarkable individual variation in Mechanitis isthmia.

Fig. 79. Thyridia psidii, an example of the "Ithomia" type of coloration. See p. 213, and Plate **4**, Fig. 47.

Fig. 80. Napeogenes cyrianassa, showing semi-translucent condition of wings. See p. 213.

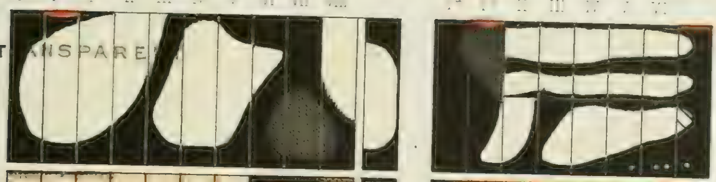
Fig. 81. Ceratinia vallonia.

Fig. 82. Melinaea parallelis; albinism of spots on primaries; black band of hind wing broken in the middle. See p. 188, 213.

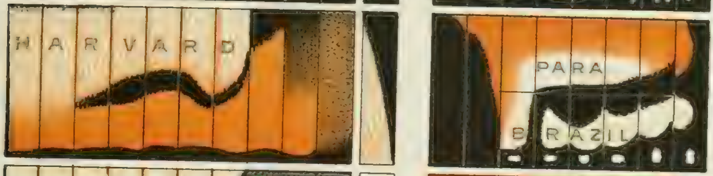
Fig. 83. Ceratinia leucania, which probably mimics M. parallelis.

Figs. 84–87. Mechanitis isthmia, showing remarkable individual variation in the black stripe of the hind wings, and also in the "inner yellow" spot of the fore wings. See p. 184, 213.

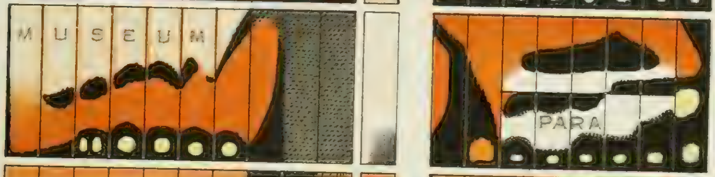
HIND WING FORE WING


TRANSPARENT

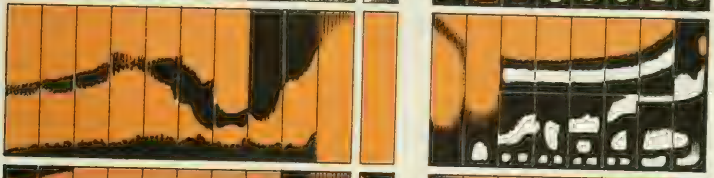
79. *Thyridia psidii Linn.*


HARVARD
PARA
BRAZIL

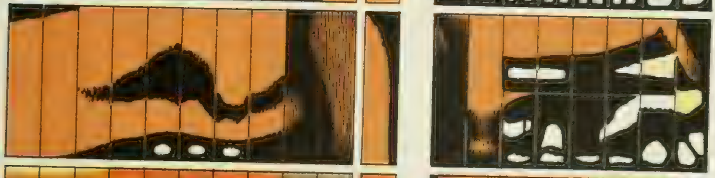
80. *Napeogenes cyrianassa Doubl. & Hew.*


MUSEUM
PARA

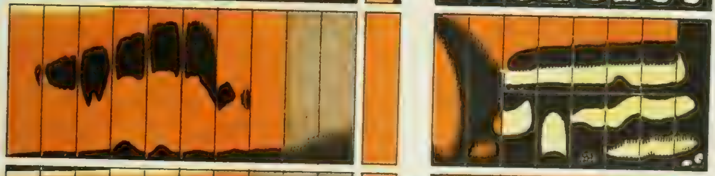
81. *Ceratinia vallonia Hew.*



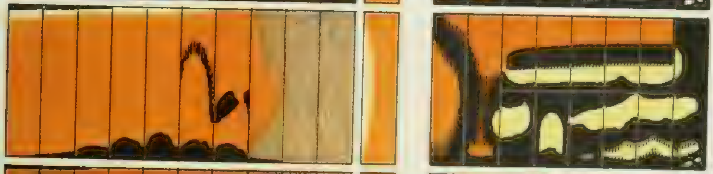
82. *Melinaea parallelis Butl.*



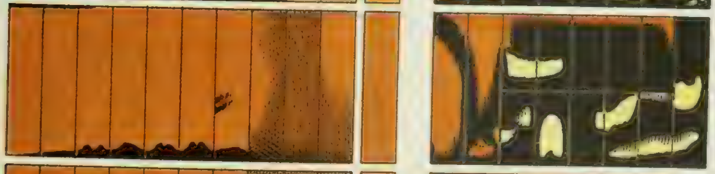
83. *Ceratinia leucania Bates.*



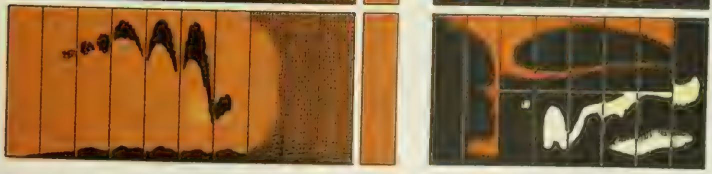
84. *Mechanitis isthmia Bates.*



85. *Mechanitis isthmia Bates.*



86. *Mechanitis isthmia Bates.*



87. *Mechanitis isthmia Bates.*

A. G. M. del.

PLATE 8.

Illustrates the mimicry between members of the "Sylvanus" group of the genus Heliconius and various Melinaeas, etc.

Fig. 88. Heliconius eucoma, an example of the "Sylvanus" type of coloration in genus Heliconius. See p. 214.

Figs. 89, 90. Heliconius dryalus and Melinaea paraiya; close resemblance of their color-patterns. See p. 214.

Figs. 91, 92, 93, 94. Respectively Heliconius eucrate, Melinaea thera, Eueides dianasa, and Mechanitis polymnia; showing close resemblance between color-patterns. See p. 214.

Figs. 95, 96. Heliconius sylvana and Melinaea egina; these two forms are said by Bates to mimic each other. See p. 214.

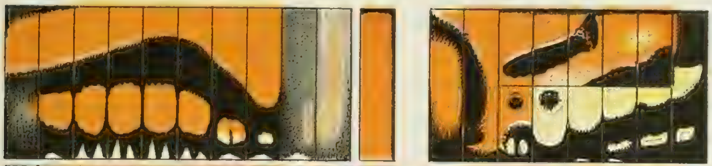
HIND WING

I^a I^b I^c II III IV V VI VII VIII

FORE WING

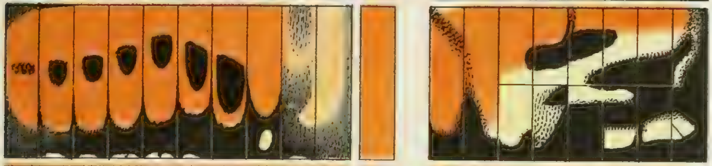
I^a I^b II III IV V VI

88.



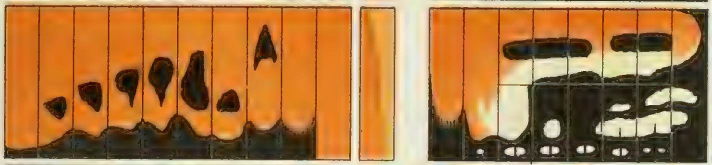
Heliconius eucoma Hübn.

89.



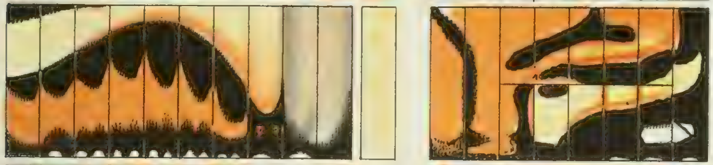
Heliconius dryalus Hopff.

90.



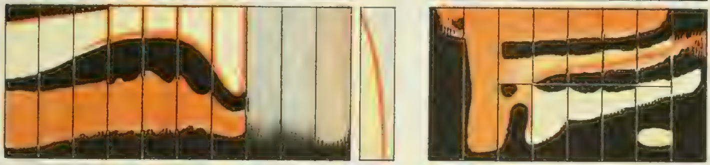
Melinaea paraiya Reak.

91.



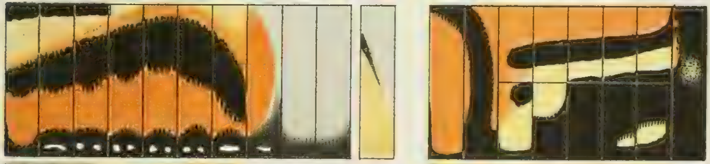
Heliconius eucrate Hübn.

92.



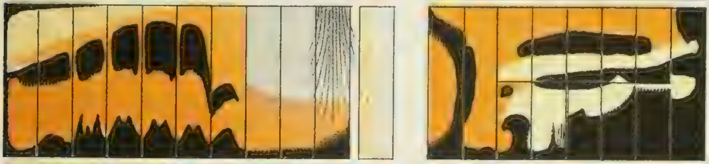
Melinaea thera Feld.

93.



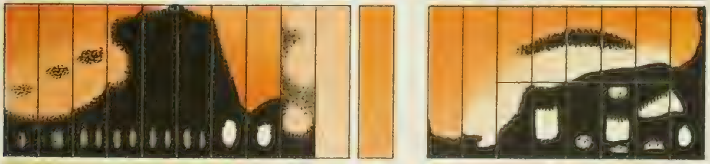
Eueides dianasa Hübn.

94.



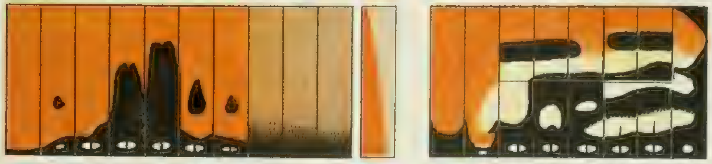
Mechanitis polymnia Linn.

95.



Heliconius sylvana Cram.

96.



Melinaea egina Cram.

PLATE 9.

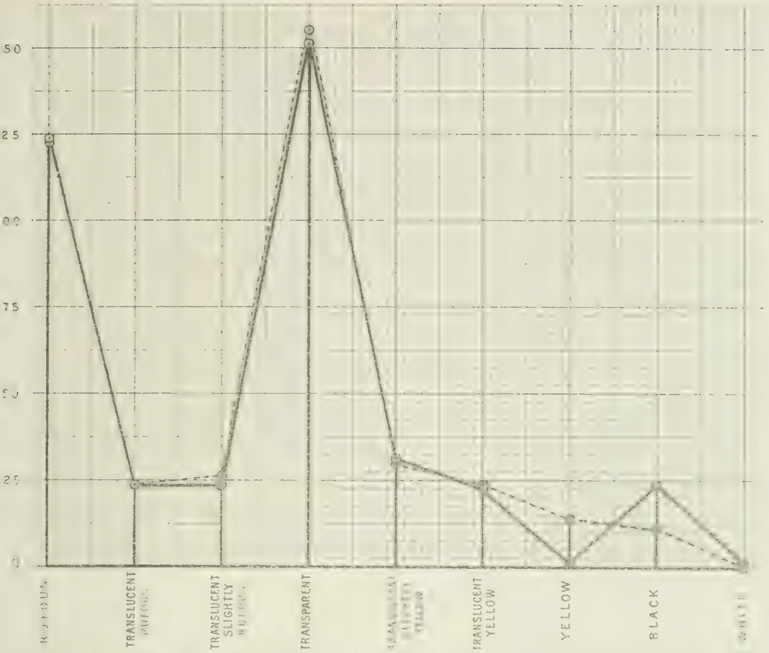
Diagrams to illustrate color-variations.

The various colors are laid off at definite intervals along the axis of abscissae. and the ordinates represent the number of species which exhibit the various colors.

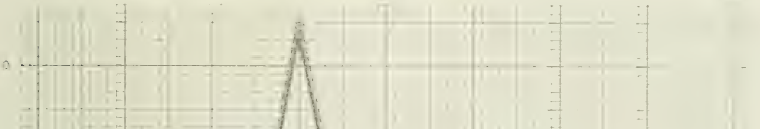
Fig. 97. Represents the color-variations of the "inner rufous" area of the fore and hind wings in the Danaoid Heliconidae. The full line represents the variations of the *fore* wing. The dotted line those of the *hind* wing. The closeness of these two lines shows the intimate relations between the color-variations of the "inner rufous" areas upon fore and hind wing. See p. 218.

Fig. 98. The full line represents color-variations of "inner yellow" spot of fore wings in Danaoid Heliconidae. The dotted line represents same for "middle yellow." It is apparent that the "inner yellow" is more variable than the "outer yellow," and also that the variations of both are quite similar to those of the "inner rufous." See p. 219.

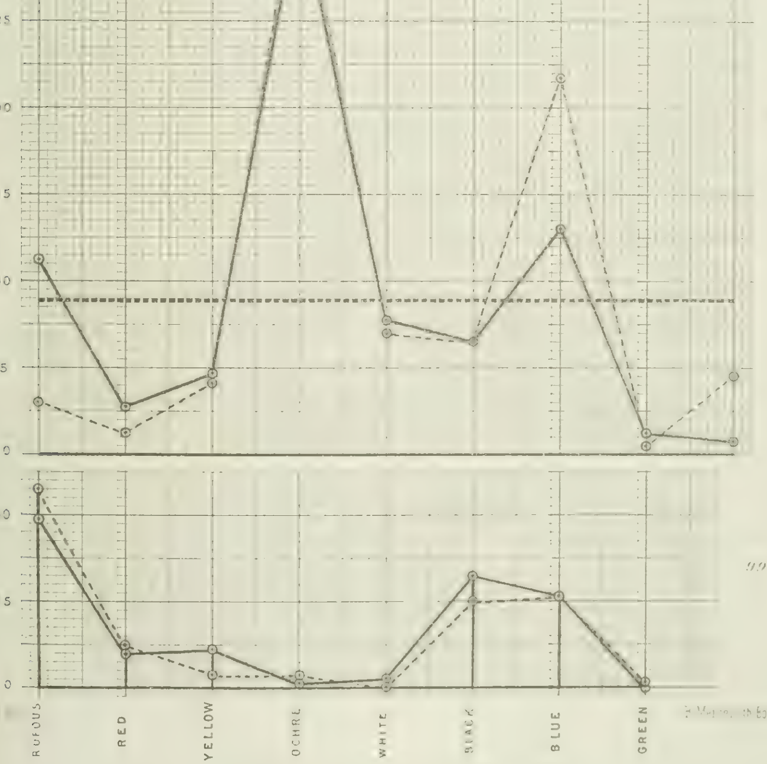
Fig. 99. Color-variations of "inner rufous" areas of Acraeoid Heliconidae. The full line represents the fore wing and the dotted line the hind wing. See p. 218.



27.



28.



29.

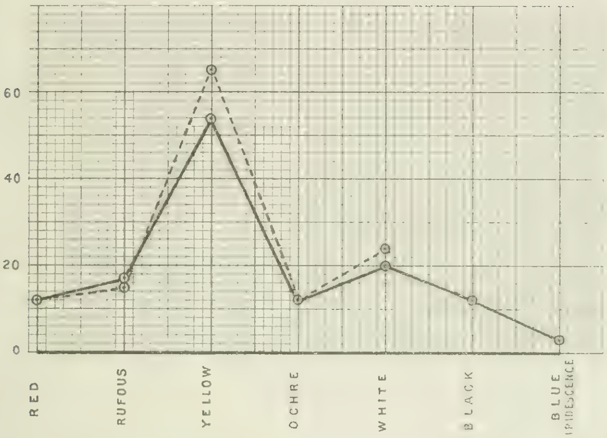
B. Meisel, lith Boston.

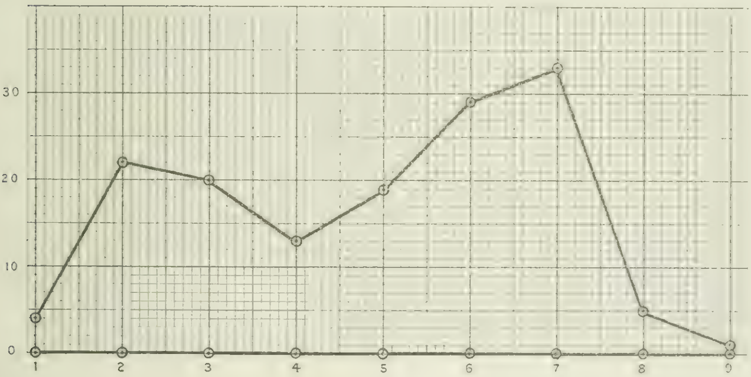
PLATE 10.

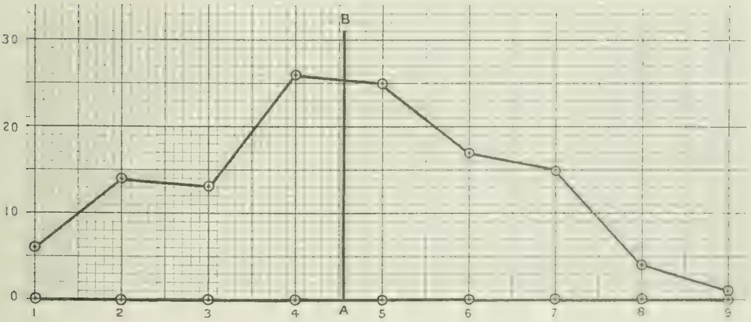
Fig. 100. Color-variations of "inner yellow" spots on fore wings of Acraeoid Heliconidae. The full line represents the "inner yellow," the dotted line the "middle yellow." See p. 221.

Fig. 101. Variations of marginal spots upon fore wing in Danaoid Heliconidae. These spots tend to appear either as 2 or 3, or as 6 or 7 spots. See p. 223.

Fig. 102. Variations of marginal spots of hind wings in Danaoid Heliconidae. These spots tend to appear either as 4 or as 5 spots. See p. 223.







B. Meisel lith Boston.

No. 5. — *The Mesenteries and Siphonoglyphs in Metridium marginatum Milne-Edwards.* By G. H. Parker.[1]

Introduction.— Since the publication of the Hertwigs' ('79) paper on the anatomy of the actinians, the attention of investigators has been more and more directed toward the details of the internal structure of these organisms. This new departure has been conducted in the main on the lines of systematic zoölogy, and, though its advocates in the beginning may have been somewhat Utopian in their expectations, it has certainly carried our understanding of the natural relations of this group of animals a long step forward. The new features thus introduced into the classification have, however, been subject to frequent modification, and every actinian newly investigated may be expected to exert some influence on the classification finally adopted. It is to be regretted that much of this kind of investigation has been of necessity carried out on a limited, often a very limited, number of specimens, so that the possible error of regarding individual variations as characteristic of large groups is not always eliminated.

The following pages contain a record of certain structural peculiarities in a single species of actinian, the common *Metridium marginatum* Milne-Edwards of our coast, as represented by a considerable number of specimens. As this record shows, uniformity of structure is by no means a general characteristic of this species; hence these observations are to some extent a contribution to the study of the variability of this animal.

The material on which the following observations were made consisted of 131 adult specimens of *Metridium marginatum.* These were collected in part by myself and in part by my laboratory assistant, Mr. J. I. Hamaker, to whom I am under obligations for this kindness. All the specimens came from the neighborhood of Newport, R. I., and were prepared and to some extent studied in Mr. Alexander Agassiz's Laboratory at that place. I here wish to express my thanks to Mr. Agassiz for the privilege of carrying on this work at the Newport Laboratory.

---

[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXV.

The specimens were prepared by the Tullberg ('91) method, which consists in stupefaction by the gradual introduction of magnesic sulphate into the water containing the actinians, and in subsequent hardening by means of chromic acid. This method, when properly employed, yields beautifully expanded and thoroughly hardened specimens, and my experience with it has been such that I can fully indorse the recommendations given it by Tullberg ('91), Carlgren ('93, p. 7), and others. Specimens prepared in this way were cut transversely with a common razor, and the number and arrangement of the mesenteries and siphonoglyphs[1] were recorded. Owing to the large size of the specimens, this could be easily done under the magnification of an ordinary hand lens.

Siphonoglyphs. — The Hexactinia, to which Metridium belongs, were until recently supposed to possess always two siphonoglyphs; but this surmise has been shown to be not well grounded, and, in the species under consideration, as McMurrich ('91, p. 131) has already pointed out, either one or two siphonoglyphs may be present. In the 131 specimens that I examined, 77 (or about 59 per cent) had only *one* siphonoglyph (Fig. 3), 53 (or about 41 per cent) had *two* siphonoglyphs (Fig. 1), and a single specimen possessed *three* such organs (Fig. 6). In no instance was a specimen found without a siphonoglyph. The smooth surface of the siphonoglyph is so strongly contrasted with the longitudinally ribbed surface of the rest of the œsophagus that in none of the specimens examined was there any uncertainty as to the number of siphonoglyphs present. The striking difference between these two kinds of surface cannot be made to appear so clearly in the figures as it did in the actual specimen, where, in addition to the cut face, the natural face of the œsophagus could also be inspected. McMurrich ('91, p. 131) remarks that in the individuals examined by him, those with one siphonoglyph were almost, if not quite, as frequent in occurrence as those with two, but in my enumeration it will be seen that they were really somewhat more numerous.

Since only one of the 131 specimens possessed three siphonoglyphs, it is obvious that this condition may be set aside as distinctly exceptional, and, further, since the other specimens were almost equally divided between those with one and those with two siphonoglyphs, these conditions may fairly be considered typical. It will be convenient in the subsequent discussion to designate these two types by special names, and I shall call that characterized by one siphonoglyph the *monoglyphic* type, and that by two the *diglyphic* type.

---

[1] The term "siphonoglyphe" was first introduced into zoölogical nomenclature by Hickson ('84, p. 694), and has since been widely accepted. Professor Hickson kindly informs me that the last syllable of this term is derived from the Greek word γλυφίς, which in the plural form, γλυφίδες, has been used to signify the grooves on an arrow for the insertion of the feathers. The root of this word appears to call for no final *e*, and since in making English words it is best, as Professor Hickson remarks, to use only roots, I therefore propose to change the spelling of the term in question by omitting the final *e*, and to this Professor Hickson assents.

Variations in the number of siphonoglyphs have already been recorded in other actinians. Thus, besides the observations of McMurrich already alluded to, Thorell ('59, Tab. I. Figs. 1 and 2) figured and described specimens of *Metridium dianthus* either with one or with two siphonoglyphs. The monoglyphic condition was also recognized for this species by Gosse ('60, p. 12), who, in ignorance of Thorell's observations, supposed this condition to be characteristic of the species, a mistake afterwards corrected by Foot ('63, p. 64). The presence in some specimens of one, and in others of two siphonoglyphs in *M. dianthus*, as first asserted by Thorell, has recently been confirmed by G. Y. and A. F. Dixon ('91, p. 19), and by Carlgren ('93, p. 104). Furthermore, the Dixons and Carlgren agree in stating that, though two siphonoglyphs may be present in this species, one is the rule. G. Y. and A. F. Dixon ('91, p. 20), moreover, have recorded one specimen of *M. dianthus* with three siphonoglyphs.

Representatives of the genus Sagartia also show variations in the number of their siphonoglyphs; thus G. Y. Dixon ('88, p. 120) observed that in *Sagartia venusta*, *S. nivea*, and *S. mineata*, either one or two siphonoglyphs may be present. The same is probably true of *S. rosea* (cf. F. Dixon, '88, p. 139), and of *S. lactea* (cf. McMurrich, '94, p. 177). In specimens of *Bunodes thallia*, studied by G. Y. and A. F. Dixon ('89, p. 318), one, two, three, and even four siphonoglyphs were observed, although in each of twenty-three adult specimens of *B. verrucosa* the same authors ('89, p. 322) found regularly two siphonoglyphs. Finally Blochmann and Hilger ('88, p. 391) described a specimen of Gonactinia in which traces of a third siphonoglyph seem to have been present.

It is evident from the foregoing account that in several actinians besides Metridium a variation in the number of siphonoglyphs is not unusual, though this variation may not be so pronounced as to constitute a structural type. The importance of these peculiarities from a systematic standpoint has already been appreciated, and in the more recent definitions of the Hexactinia the statement is made that these actinians possess two siphonoglyphs (occasionally one), thereby recognizing the monoglyphic and diglyphic types as normal.

Mesenteries. — In *Metridium marginatum* the pairs of mesenteries are attached lengthwise to the wall of the column, and either reach the œsophagus and unite with it (complete mesenteries) or fall short of that structure (incomplete mesenteries). Of the pairs of complete mesenteries the two usual kinds can be distinguished: those whose longitudinal muscles face the exocœls (directive mesenteries) and those whose longitudinal muscles face the endocœls (non-directive mesenteries).

The *directive mesenteries* are remarkable for the constancy of their relations to the siphonoglyphs. To each siphonoglyph is attached a single pair of directives, and in no instance among the 131 specimens examined was an exception to this rule found. In the monoglyphic type (Figs. 3, 4, 5, 7, and 8) one pair, and only one pair, of directives was present; in the diglyphic type (Figs. 1 and 2) two pairs were invariably observed; and even the single specimen with three siphonoglyphs (Fig. 6) formed no exception, but exhibited three pairs of directives.

This exact correlation between the number of siphonoglyphs and of directives, which probably also obtains in other species of Metridium (cf. Carlgren, '93, p. 106), as well as in the allied genus Sagartia (cf. F. Dixon, '88, p. 136), is rather striking, because the two sets of structures concerned are not invariably thus associated in all actinians. For instance, in Peachia and Oractis (cf. McMurrich, '91, pp. 135, 137), though two pairs of directives are present, only one siphonoglyph occurs; and in Ptychodactis (cf. Appellöf, '94, pp. 5, 7), though two pairs of directives can be seen, no siphonoglyphs are observable. These instances serve to show that in some actinians directive mesenteries may occur without siphonoglyphs, and thus they render more striking the correlation between the variations of the directives and of the siphonoglyphs in *Metridium marginatum.*

The *non-directive mesenteries* vary so much in their number and arrangement that they can best be considered in connection with the particular types with which they occur. In the diglyphic type (53 specimens), in addition to the two pairs of directives, there may be from four to ten pairs of non-directives. The frequency of the occurrence of the different numbers of pairs is indicated in the following table: —

Diglyphic Type (two siphonoglyphs and two pairs of directives).

Pairs of Non-directives	4	5	6	7	8	9	10
Number of Cases observed . .	40	4	3	3	2	0	1

In this type (Fig. 1) the two pairs of directives of course divide the non-directives into two groups. I regret that, before it occurred to me to determine the number of mesenteries in each of these two groups for the 53 specimens of this type, some of the specimens were so far dissected as to render them no longer serviceable for this enumeration. I can therefore make a statement concerning this division in the cases of only twenty specimens.

Groups of Non-directives . .	1 + 7	2 + 2	2 + 3	2 + 4	2 + 5	2 + 6	4 + 6
Number of Cases observed .	1	10	2	2	3	1	1

In comparing these results, it will be observed, first, that the great majority of individuals (40 in 53) possess four pairs of non-directives, and, next, that the arrangement of these non-directives in ten cases out of twenty is in two groups of two pairs each. This symmetrical arrangement of the four pairs of non-directives in the diglyphic type reproduces the assumed typical Hexactinian arrangement, and, since the representatives of the other variations are comparatively so few in numbers, this may be taken to be the only characteristic condition of the diglyphic type.

In the monoglyphic type (77 specimens), in addition to the one pair of directives, there were from three to fourteen pairs of non-directives. The frequency of their occurrence is shown in the following table: —

Monoglyphic Type (one siphonoglyph and one pair of directives).

Pairs of Non-directives . .	3	4	5	6	7	8	9	10	11	12	13	14
Number of Cases observed .	1	4	20	19	21	5	1	4	1	0	0	1

Admitting the monoglyphic type to be derived from the diglyphic by the conversion of a pair of directives into a pair of non-directives, one would expect the monoglyphic type with five pairs of directives to be most often met with. Such, however, is not the case, for specimens with six or seven pairs of non-directives are about as numerous as those with five. Since any of the three groups with five, six, or seven pairs of non-directives is represented by a greater number of individuals than all the other minor groups of variations taken collectively (cf. Table of Monoglyphic Type), it is clear that in the monoglyphic type there are three structural subtypes characterized respectively by five, six, and seven pairs of non-directives, instead of only a single such subtype, as in the diglyphic condition. These relations indicate a certain degree of distinctness between the diglyphic and the monoglyphic type; for the monoglyphic has obviously a greater range in variation, as shown in its three subtypes, than the diglyphic with only a single one. It is an interesting fact in this connection, that the monoglyphic subtype with six pairs of non-directives often repeats (Fig. 4), so far as its complete mesenteries are concerned, the arrangement of mesenteries found in Scytophorus, for which R. Hertwig ('82, p. 104) constructed a separate family, the Monauleæ.

It might at first be suspected that the three monoglyphic subtypes pointed out above, and in fact all the variations in the number of complete mesenteries, could be explained on the assumption that certain incomplete mesenteries by excessive growth had become complete, or that complete ones had become incomplete, thus introducing a variation in the number of complete mesenteries, without, however, altering the total number of all kinds of mesenteries; but in the individuals examined the relative development of the incomplete mesenteries was found to be subject to so much variation that the satisfactory determination of the total number of mesenteries as a basis of comparison was practically impossible, and all attempts to carry through interpretations such as that suggested above resulted in such ambiguous and strained results that the unnaturalness of the method condemned it. Moreover, in the monoglyphic type with *six* pairs of non-directives (Fig. 4), incomplete as well as complete mesenteries are sometimes so symmetrically placed that no attempt to readjust them is warranted. What may be said of such cases is, that, in place of the usual five pairs of non-directives, six pairs are present, and this increase cannot be ascribed to reinforcement from the ranks of incomplete mesenteries. Such cases as these are so frequent, and instances that may be interpreted as the conversion of complete into incomplete mesenteries or the reverse are so few, that it must be admitted, I believe, that these differences are due much more frequently to fundamental differences in the plans on which the mesenteries of different individuals are laid down than to the more easily conceived relation between complete and incomplete mesenteries.

The *incomplete mesenteries* have not been exhaustively investigated. Their great number, variability in size, and the frequent difficulty met with in attempting to classify them, render such a task nearly impossible. In what are generally assumed to be the more typical specimens of Metridium (Fig. 1), an exocœl may contain one pair of secondary mesenteries, two pairs of tertiaries, four pairs of quarternaries, and evidences (ridges) of eight pairs of quinaries. Though this condition was occasionally realized, in the great majority of cases irregularities in what are presumably secondaries and tertiaries, not to mention higher orders, were so numerous that consistent tabulation was out of the question. So far as size and position were concerned, what seemed to be secondaries showed such variations that no two specimens in which the arrangement of the complete mesenteries agreed, had similar arrangements of the secondaries, except in six instances of the 40 typical diglyphic specimens; and each of these six instances showed variations in the tertiaries characteristic of it as an individual. So far, then, as the incomplete mesenteries are concerned, we soon reach groups of variations by which individuals may be characterized; in other words, if the variations of the primaries (complete mesenteries), secondaries, and tertiaries be considered together, it will be seen that no two of the 131 specimens examined were alike, each one having a combination of variations peculiar to itself. This is, perhaps, the most important feature in the variations of the incomplete mesenteries.

That variations in the number of mesenteries, such as have been pointed out in the preceding paragraphs, occur in other actinians is well known. Thus Carlgren ('93, p. 106) states that in *Metridium dianthus,* in addition to a single pair of directives, six, seven, or even nine pairs of non-directives may occur, and F. Dixon ('88) has shown that in several species of Sagartia the number of non-directives may reach twelve or even sixteen pairs. Further, in four specimens of *Bunodes thallia,* G. Y. and A. F. Dixon ('89, pp. 317, 318) found respectively 15, 19, 21, and 26 pairs of non-directives. These citations suffice to show that extensive variations in the mesenteries may occur in other actinians than *Metridium marginatum,* but the cases recorded for any one species are so few that generalizations cannot be drawn from them.

As a rule, variations in the mesenteries occur in both members of a pair in the same way, but not infrequently one finds pairs in which the two members are not equally developed. When this occurs amongst the complete or nearly complete mesenteries, it may result in the formation of a pair one member of which is complete and the other incomplete (Fig. 2). The 131 specimens of Metridium examined possessed in all 739 pairs of non-directives, and, of these, 17 pairs (or about 2.4 per cent), distributed through thirteen individuals, possessed each an incomplete member. Of the thirteen individuals exhibiting this variation, ten were of the monoglyphic type, and three of the diglyphic type. In the monoglyphic type it is customary to assume that the single siphonoglyph present corresponds to the so-called ventral one of the diglyphic condition. This assumption is at least convenient, for it allows us to distinguish in each pair of lateral non-directives a dorsal and a ventral member. Admitting this distinction for the sake of description, it may be said that seven of the ten monoglyphic specimens had each a single pair of non-directives in which one member was incomplete, and of these incomplete mesenteries four were dorsal, two were ventral, and one was indeterminable (Fig. 8); and that the three remaining monoglyphic specimens had each two such pairs, of which in one instance both the incomplete mesenteries were dorsal, and in two instances one was a dorsal and the other a ventral mesentery (Fig. 7). Thus in the ten monoglyphic specimens, this variation was observed in thirteen pairs of mesenteries, of which eight presented incomplete dorsal members, four incomplete ventral members, and one was indeterminable. It is evident that this variation is not limited to either dorsal or ventral members, and is not correlated with the fact that in many actinians ventral members, as a rule, develop later than dorsal ones; in other words, this variation is probably not to be regarded as atavistic.

In the adult condition of the diglyphic type, I see no way of distinguishing dorsal from ventral, and the most that can be said of the three cases of variation met with under this type is that in two of them only one mesentery each was incomplete (Fig. 2), while in the third two were incomplete. In the latter case the two mesenteries (as in Fig. 7) were not on corresponding sides; hence one of them must have been dorsal and the other ventral, but exact determination could not be made. The variations in the diglyphic type, then, present no essential features not already met with in the monoglyphic type.

Many pairs of mesenteries in which both members are incomplete show variation of the kind indicated above, in that one member is larger than the other (Fig. 4), but because of the extreme variability of these parts no record has been kept of such variations.

In a few cases *single* mesenteries have been observed (Fig. 2). These, as the arrangement of the longitudinal muscles of their neighbors shows, have absolutely no trace of a mate. In the instance figured, it is difficult to decide which of the two mesenteries, the complete (y) or the incomplete (x), is the single one. One or other must be. Single mesenteries as exceptions have already been recorded by F. Dixon ('88, p. 138) in Sagartia, and by Carlgren ('93, p. 106) in Metridium.

Among the complete mesenteries, two cases of union by what would have been the median margins of the participants have been observed (Fig. 8). An instance of this kind has already been recorded by R. Hertwig ('82, p. 37) in Tealia, and in this, as in Metridium, the united mesenteries were not members of the same pair, but of adjacent pairs.

No instances of the occurrence of longitudinal muscles on both the exocœl and the endocœl face of the same mesentery, as observed by McMurrich ('89, p. 30) in Aulactinia, have been noticed.

So far as the mutual arrangement of complete and incomplete mesenteries is concerned, the monoglyphic and diglyphic types show rather characteristic differences. In the diglyphic type the complete mesenteries usually show no special tendency to collect at one pole or the other of the animal (cf. Fig. 1). In the monoglyphic type there is often a marked tendency for all but two pairs of the non-directives to collect opposite the directives (cf. Fig. 5); consequently the half of the animal centering about the directives has an arrangement of parts like that found in the corresponding half of a diglyphic animal, while the other half contains a more or less crowded group of non-directives. In this respect Metridium seems to differ from Sagartia, in which, according to the figures given by F. Dixon ('88, Plate I.), such a crowding of non-directives is not noticeable. This condition recalls in a superficial way that found in Cerianthus, in which an active growth of mesenteries takes place opposite the siphonoglyph.

The characteristic arrangements of the mesenteries in connection with the monoglyphic and diglyphic types probably recur under similar conditions in *M. dianthus;* for such arrangements have been figured by Thorell ('59, Tab. I. Figs. 1 and 2) and briefly described by Carlgren ('93, p. 106).

While the crowding of the mesenteries occurs as a rule only in monoglyphic specimens of Metridium, one instance of it has been observed in a diglyphic specimen (Fig. 2), and here the general resemblance to the specimen with three siphonoglyphs (Fig. 6) is so striking that I have felt almost justified in interpreting this specimen as a triglyphic animal, at one pole of which the directives, with the loss of the siphonoglyph, had given place to a group of non-directives.

In the preceding account I have intentionally avoided, as far as possible, the use of the terms dorsal and ventral as applied to the two poles of the actinian's body. This has not been because of objections that might well have been raised against these terms in themselves, as Haddon ('89, p. 300) has done, but because of the more fundamental question of whether dorsal and ventral can really be distinguished in an adult Metridium. These terms, as is well known, may be applied with perfect precision to the adults of forms like Edwardsia, where the longitudinal muscles bear very unlike relations to the two poles of the animal; but in forms like the diglyphic type of Metridium (Fig. 1), where the muscles of the pairs of non-directives are similarly related to both poles, this means of distinguishing dorsal and ventral is lost. It has been suggested that even in cases of this kind dorsal and ventral may still be distinguished, either by the conditions of the siphonoglyphs, — the ventral being better developed than the dorsal (Faurot, '95, p. 62), — or by the condition of the subsidiary mesenteries, — the more dorsal pairs, because of their earlier development, remaining larger than the ventral ones (Carlgren, '93, p. 100). Unfortunately, these criteria, even supposing them to be true, which is by no means certain, cannot be employed on the diglyphic type of Metridium because of the similarity of its two poles. So far as the adult diglyphic Metridium is concerned, I am obliged to confess that I can find no satisfactory criteria for the determination of dorsal and ventral relations.

With the monoglyphic type the case seems simpler. It is generally stated that, when only one siphonoglyph is present, it is the ventral one; but, as Carlgren ('93, p. 100) remarks, so far as Sagartia is concerned, this statement has never been accompanied with any direct proof; nor, I may also add, has it been proved for Metridium. The argument used by McMurrich ('91, p. 133) to show that the single siphonoglyph in the monoglyphic Metridium is the ventral one may be used with equal accuracy to show that this siphonoglyph is the dorsal one, for the argument advanced rests upon the sequence of the development of the mesenteries, which, being unknown in Metridium, has simply been assumed by McMurrich. The case of Metridium seems to be precisely like that of

Sagartia, in which, as Haddon ('89, p. 300) remarks, it seems impossible, in our present state of knowledge, to determine dorsal and ventral relations. It is probable that this determination can be made only after the sequence of development of these mesenteries has been discovered. In the four types of sequence thus far known (cf. Fowler, '94, p. 470), the ventral directives are always the third pair of mesenteries to form, and the dorsal directives either the second or fourth. It is probable that, when the developmental sequence of the mesenteries is discovered for the two types of Metridium, the determination of dorsal and ventral in this actinian will be made with as much certainty as in any other, and we shall probably then know whether in the monoglyphic type the single siphonoglyph is a dorsal one, a ventral one, or in some specimens one and in others the other.

Before concluding this account of the mesenteries in Metridium, I wish to consider briefly some other aspects of the monoglyphic and diglyphic types. When I first perceived that there were two structural types in Metridium, I suspected that they might be correlated with sexual differences. To test this question, I determined the sexes of a number of individuals of each type. In ten monoglyphic specimens, five were females and five were males; in twenty-seven diglyphic specimens, fifteen were females and twelve were males. Evidently the two types are not correlated with difference in sex.

The fact that the two sexes occur in about equal numbers under both types suggests that these two types may in reality be two varieties of the species *Metridium marginatum.* In support of this opinion, it may be mentioned that the two types show a difference in the degree of their variability, the diglyphic type having only one subtype, the monoglyphic three; and, further, that, while the diglyphic type presents usually a rather typical Hexactinian arrangement of mesenteries, the monoglyphic type shows a general tendency to crowd the non-directive mesenteries to the region opposite the one siphonoglyph.

These differences, however, fairly marked as they are, are insufficient in my opinion to warrant the assumption that the two types are really varieties, and the determination of this question must wait, I believe, till more is known of the breeding habits of Metridium. If it can be shown that in the offspring of one animal representatives of both types occur, the idea that we are dealing with varieties could not be maintained, and the species could at most be said to be dimorphic. If, however, the types could be shown to breed true, they might with justice be described as varieties.

Should these types prove not to be of the value of varieties, they may still possibly be correlated with the methods of reproduction. Besides the sexual method, *Metridium marginatum* reproduces non-sexually by small buds cut off from the margin of the animal between its aboral disk and its column. This method of reproduction, long ago hinted at by Verrill ('69, p. 257), can usually be seen taking place in any large specimen. Similar conditions have been observed in *Metridium dianthus* by G. Y. and A. F. Dixon ('91, p. 20), and by Carlgren ('93, p. 108). Possibly the two types here described are the products, one of the sexual, the other of the non-sexual, method of reproduction. The solution of this question, however, must be left to future investigation.

CAMBRIDGE, January 9, 1897.

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EXPLANATION OF PLATE.

All figures represent transverse sections of the column of *Metridium marginatum* Milne-Edwards. In each case all the complete mesenteries have been drawn, and in some instances a few of the incomplete ones. All figures are magnified about 1.5 diameters.

Fig. 1. Diglyphic specimen, showing typical hexamerous arrangement of the complete mesenteries, and a regular group of subordinate mesenteries in a primary exocœl.

Fig. 2. Diglyphic specimen, showing a very irregular arrangement of the complete mesenteries, one group of which resembles the crowded group of mesenteries found opposite the directive pole in the monoglyphic type. In this crowded group occurs an unpaired mesentery (x or y).

Fig. 3. Monoglyphic specimen, with five pairs of non-directives, showing the regular arrangement of the subordinate mesenteries about the pair of non-directives opposite the directive pole.

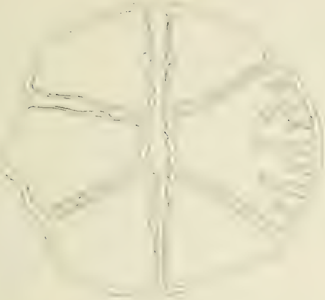
Fig. 4. Monoglyphic specimen, with six pairs of non-directives, showing the regular arrangement of the subordinate mesenteries about the two pairs of non-directives opposite the directive pole.

Fig. 5. Monoglyphic specimen, with ten pairs of non-directives, showing the crowding of the non-directives in the region opposite the directive pole.

Fig. 6. Triglyphic specimen.

Fig. 7. Monoglyphic specimen, showing pairs of mesenteries in which dorsal as well as ventral components are incomplete.

Fig. 8. Monoglyphic specimen, showing the union of two primary mesenteries.



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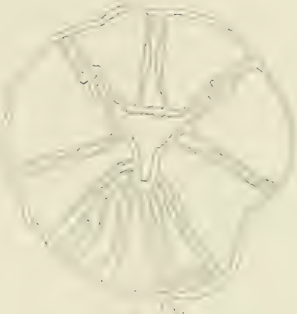

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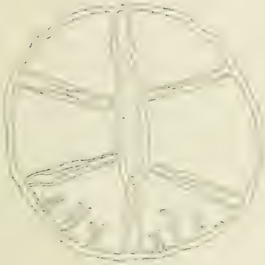

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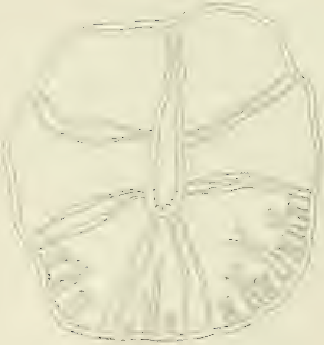

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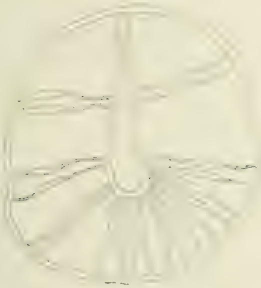

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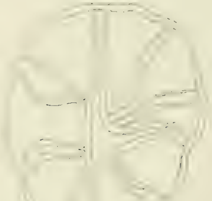

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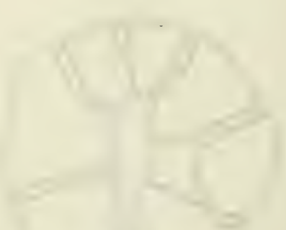

8.

No. 6. — *Photomechanical Changes in the Retinal Pigment Cells of Palæmonetes, and their Relation to the Central Nervous System.*

By G. H. Parker.[1]

Contents.

Page
Introduction 275
Structure of the Eye in Palæmonetes 276
Photomechanical Changes in Normal Retina 278
  1. Methods 278
  2. General Changes in Retina . 279
  3. Changes in Proximal Retinular Cells 279
  4. Changes in Accessory Cells . 281
  5. Changes in Distal Retinular Cells 284
  6. Summary of Changes in Normal Retina 288
Sympathetic Photomechanical Changes 289
Localized Photomechanical Changes 290
Photomechanical Changes in Excised Eyes and Retinas . . . 291
General Summary 295
Note 297
Papers Cited 299
Explanation of Plate.

Introduction.

The present paper is a record of a series of experiments on the photomechanical changes in the pigment cells of the retina in *Palæmonetes vulgaris* Stimp. This species is especially favorable for such work, since its retina exhibits in a marked degree all the kinds of pigment changes that have thus far been observed in the eyes of crustaceans.

Those that have worked upon this subject have, in the main, followed in the lines laid down by Boll, Engelmann, and others in their studies on the eyes of vertebrates. Although the pigment changes in vertebrates are relatively simple, they are, even now, far from being satisfactorily understood, and it is therefore not surprising that in the arthropods, where the pigment changes of the retina are probably more complex than in any other group of animals, much still remains to be done. There has been a tendency, moreover, among some of those that have studied such phenomena, to generalize on observations taken from eyes of totally different types, such as the compound eyes of insects and the simple eyes of arachnids; and this tendency, though in a measure justifiable, has led, I believe, to a want of attention to the characteristic differences of the pigment changes in each given type of eye, a matter that, in my opinion, lies at the foundation of any satisfactory understanding of these changes. What is most needed at present, therefore, seems to be a thorough and exhaustive study of the pigment changes of each of the more important types, rather than an inspection, necessarily more or less superficial, of the various arthropod eyes that have not as yet been examined. The following studies have been made with the hope that they would contribute in this respect to a more complete understanding of the pigment changes in the compound eye, especially in crustaceans.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXVI.

The earliest paper on the pigment changes in compound eyes, so far as I am aware, was published in 1889 by Exner ('89), and contains in a condensed form the essential peculiarities of the pigment changes in the compound eyes of certain insects. In 1890 Stefanowska ('90) published an account in which this subject was again considered, but with a wider range of material. In the next year three contributions appeared: Exner's ('91) brilliant and important essay on the physiology of compound eyes, of which his former publication had been in the nature of a partial preliminary notice; Szczawinska's ('91) article on the pigment changes in the eyes of crustaceans and arachnids; and Herrick's ('91) account of similar changes in the eyes of Palæmonetes, contained in his monograph on the development of Alpheus. Three years later Kiesel ('94) described some very noteworthy observations on the pigment changes in the eyes of insects. The following year the writer (Parker, '95) published, in connection with other matters, an account of the retinal pigment changes in Astacus, and a preliminary statement of the results given in full in this paper was published last year (Parker, '96). These, I believe, are all the publications in which the questions here raised have been considered. Critical comments on their contents will be found in the following pages.

STRUCTURE OF THE EYE IN PALÆMONETES.

Before describing the pigment changes in the retina of Palæmonetes, it will be necessary to outline briefly the structure of the eye in this animal. The eye may be said to be that portion of the optic apparatus contained in the optic stalk. It consists of a retina, at the distal end of the stalk, and a series of four optic ganglia, which extend through the axial portion of the stalk. The retina is connected with the first optic ganglion by the retinal nerve fibres. Nerve fibres connect the first optic ganglion with the second, the second with the third, and the third with the fourth. From the fourth optic ganglion, which is situated near the proximal end of the stalk, the optic nerve extends to the brain. The finer structure of the optic ganglia in Palæmonetes is in all probability essentially the same as in Astacus, where, as I have already shown (Parker, '95, Taf. 3, Fig. 59), each optic ganglion represents a region of interruption for the great majority of the nerve fibres that intervene between the retina and the brain.

The retina in Palæmonetes is composed of ommatidia, the structure of which has already been described at length (Parker, '91, p. 108, Pl. IX.). For convenience I add a brief summary of this description. Each ommatidium is composed of five kinds of cells. Immediately under the corneal facet (Fig. 1, *crn.*) are two corneal hypodermal cells (*nl. crn.*). The distal portion of the axis of the ommatidium is occupied by the cone (*con.*), which, as seen in transverse sections (Fig. 3, *cl. con.*), is composed of four parts. Each part contains near its distal end a nucleus (Fig. 1, *nl. con.*) and represents a cell. The four cone cells are closely applied to one another in the region of the cone proper (Fig. 3). Proximally they taper off as thick, more or less independent fibres. (Compare Figs. 1, 4, and 5.) These fibres separate and apparently terminate near the distal end of the rhabdome (Fig. 1, *rhb.*). I have been unable to trace them further, though I suspected that they might end, as in Homarus (Parker, '90, p. 14), on the basement membrane. The distal retinular cells either apply themselves to the lower portion of the sides of the cone (Fig. 2, *cl. dst.*), in which case they are so closely packed that their outlines cannot be distinguished (Fig. 3, *cl. dst.*), or they occupy a more proximal position (Fig. 1, *cl. dst.*), forming a ring around the attenuated ends of the cone cells (Fig. 5). There is, of course, one ring for each ommatidium. Each ring contains six distal retinular cells, but these rings are so constituted that each cell is at the same time a member of three rings; hence there are in reality only twice as many distal retinular cells as there are ommatidia. The proximal portion of the axis of the ommatidium is occupied by the rhabdome (Fig. 1, *rhb.*), which is surrounded by seven functional proximal retinular cells (Fig. 6, *cl. px.*), in addition to which an eighth rudimentary one is present (Parker, '91, p. 111). Each functional cell ends distally in a somewhat swollen knob containing its nucleus (Fig. 1, *nl. px.*). From this swollen end the cell extends proximally over the rhabdome, beyond which it becomes slightly attenuated, and, as a retinal nerve fibre (Figs. 1 and 7, *fbr. r.*), pierces the basement membrane (*mb. ba.*) and extends to the first optic ganglion. Here it probably terminates in a fibrillation, as has already been shown to be the case in Astacus (Parker, '95, p. 41). The accessory pigment cells (Fig. 1, *cl. sn.*) occupy the space in the deeper part of the retina. The number of these cells is not constant, but, judging from their nuclei, it is not more than one or two for each ommatidium. Proximal processes extend from these cells through the apertures in the basement membrane to the distal surface of the first optic ganglion, and distal processes may extend forward to the front faces of the distal retinular cells. Each ommatidium in Palæmonetes, then, is composed of the following cells: two corneal hypodermal cells, four cone cells, two distal retinular cells, eight proximal retinular cells (one of which is rudimentary), and a variable but small number of accessory pigment cells. Black pigment granules are contained in both the distal and the proximal retinular cells, and are limited to these cells; the whitish pigment lies exclusively in the accessory pigment cells. The seven functional proximal retinular cells are the only elements of the ommatidium that are known to have nervous connections. These brief anatomical statements may suffice as an introduction to the consideration of the pigment changes in the retina.

Photomechanical Changes in Normal Retina.

The general *method* by which the normal photomechanical action of the retinal pigment cells in Palæmonetes was determined consisted in the examination of eyes that had been kept in the light or in the dark known periods of time. For a dark chamber I used a box with a tight-fitting cover. From time to time during the course of the experiments this box was tested for its light-proof qualities by exposing in it a very sensitive bromide paper, such as is used by photographers. In all my experiments this showed complete absence of light. The top of the box was pierced by a hole, through which a piece of rubber tubing was introduced so that fluids could be poured into the box without exposing its contents to light. Two or three turns in this tube were found sufficient to prevent such light as entered the outer end of the tube from reaching the interior of the box. Living shrimps in a vessel of water were placed in the box, and the cover was carefully closed. After the expiration of the required interval, hot water was run in through the tube, and the animals were thus killed in the dark. Other killing reagents, such as corrosive sublimate, picric acid, etc., were tried, but none proved so satisfactory as water at about 80° C. The periods of exposure to dark in the first set of experiments were as follows: 1 min., 5 min., 10 min., 15 min., 30 min., 45 min., 60 min., and then at intervals of an hour up to 8 hours. It was found subsequently that the experiments need not have extended over a maximum period of more than two hours, and that intervals of about fifteen minutes were all that were needed to observe the steps of the change. From each lot of animals prepared in this way, the optic stalks were cut into sections for examination under the microscope. In a similar way, the eyes of animals that had been kept some four hours in the dark were exposed to the light for given intervals, killed, cut, and examined. In cases where it was necessary to make very accurate comparisons, the eyes of the same animal were used for the two conditions; thus, after keeping the animal a given time in the light, one optic stalk was removed, and the animal kept in the dark. At the expiration of the second interval, the second optic stalk was removed and prepared. To guard against individual variations, in every experiment the eyes of at least three animals were examined.

The only *general changes* shown by retinas subjected to light or dark were changes in the arrangement of the pigment. In other respects they were not noticeably altered. Thus, no change in thickness was observable; in one case, a left retina that had been kept in the dark measured in its middle region from the corneal cuticula to the basement membrane 263 μ, while the right retina from the same animal exposed to light measured 270 μ. In a second case, a dark left retina measured 240 μ, the light right one measuring 233 μ. The cones likewise showed no significant differences. By analogy with the perceptive elements in the vertebrate eye, one might have expected the rhabdomes, the terminal nervous organs of the crustacean eye, to shorten in the light and lengthen in the dark. I was unable to obtain evidence of such a change in Palæmonetes, and yet the conditions for the exact measurement of the rhabdomes are so unfavorable in this animal that I am by no means certain that these changes may not occur. If, however, they do take place, they must be relatively small. The observable changes induced in the retina by the absence or presence of light affect the three kinds of pigment cells, — the proximal retinular cells, the accessory cells, and the distal retinular cells. These will be considered in the order given.

The pigment in the *proximal retinular cells* forms at the base of the retina a band, called by Exner ('91, p. 62) the retinal pigment. The photomechanical changes that this pigment undergoes have already been observed in various crustaceans by Exner ('91), Szczawinska ('91), and myself (Parker, '95); and, so far as the chief facts of these changes are concerned, the accounts given by these writers are in substantial agreement. In no case, however, has the precise character of these changes been followed, nor the time needed for their completion been recorded.

In a proximal retinular cell that shows the full effect of light (Fig. 1), the black pigment granules are almost uniformly scattered from the distal end of the cell backward through its whole length, including the retinal nerve fibre, to the region of the first optic ganglion. In the body of the cell proper (Fig. 6), as well as in the retinal nerve fibre (Fig. 7), it will be observed that the pigment granules lie entirely within the limits of these structures; in other words, the black pigment of this portion of the retina is contained entirely within the proximal retinular cells. This pigment, though in the main uniformly distributed through the cell, shows regularly two slight concentrations, — one at the swollen distal end of the cell (Fig. 1), and another on the sides of the rhabdome. Small irregular concentrations may also occur in the body of the cell. In the eye subjected to light, the only part of the cell except the nucleus that is entirely free from pigment granules is a transparent axis that can be traced from the region of the rhabdome down through the body of the cell, and through the whole length of the retinal nerve fibre. This is undoubtedly the axis cylinder of the nerve fibre, which, in its passage to the rhabdome, extends through the body of the cell.

In crustaceans like Cancer (Parker, '91, p. 116, Plate X. Fig. 131), in which the proximal retinular cells are more fully provided with pigment granules than in Palæmonetes, this axis is more conspicuous.

In an eye that has been kept in the dark for several hours, the bodies of the proximal retinular cells are without trace of pigment (Fig. 2), the whole mass of black pigment being concentrated in the retinal nerve fibres, i. e. proximal to the basement membrane. Here, as in the former case, the pigment lies entirely within the limits of the retinular cell.

The transition from the dark condition to the light condition of the eye was accomplished by the following steps. In an eye that had been kept some four hours in the dark and then exposed for five minutes to the light, the arrangement of the pigment in the proximal retinular cells was indistinguishable from that characteristic for full darkness. After ten minutes' exposure to light, the pigment was found to have moved forwards to the level of the basement membrane. After fifteen minutes, it was found throughout the bodies of the cells; and, at thirty minutes, well marked concentrations had appeared about the rhabdome and at the distal end of each cell. At forty-five minutes, these concentrations were somewhat more pronounced, but after that time no further changes were observable.

The reverse change, which takes place in the dark, is accomplished in the following manner. After the animal has been in the dark fifteen minutes, the concentrations of pigment about the rhabdomes and at the distal ends of the cells have almost disappeared, though the bodies of the cells still contain an almost uniform amount of pigment throughout their whole length. After thirty minutes, much more pigment is to be found proximal to the basement membrane than distal to it, and after forty-five minutes almost all the pigment is proximal in position. At the end of an hour, the condition characteristic of darkness is fully realized.

The changes just recorded occur entirely within the limits of each proximal retinular cell. There is no reason for believing that the changes are the results of a process of pigment production in one part of the cell, and of pigment destruction in another. The observed facts, on the contrary, suggest that the pigment granules of one region in the cell are moved to another. The movement, however, is not accompanied by any noticeable change in the position or even the form of the containing cell. The pigment granules seem to be carried up and down through the cell, as though by a streaming of the cell protoplasm. A similar stability of form, accompanied with an internal movement of pigment, has been described by Ballowitz ('93, Taf. XXXVI. Fig. 12, and '93^a, p. 629) in the pigment cells of the skin of fishes.

Through the kindness of Professor F. H. Herrick, I have had the privilege of examining an interesting series of eyes taken from specimens of Palæmonetes that had been kept living in a dark chamber thirty-eight days. The pigment in the proximal retinular cells of such animals showed the condition characteristic of the dark. In an animal that had been kept in the dark for this period and then exposed to light for four hours and three quarters, the pigment returned partially to the position characteristic of the light. The greater part of it remained proximal to the basement membrane, and from that which moved into the bodies of the cells no marked concentrations were formed, either about the rhabdomes or at the distal ends of the cells. Long confinement in the dark, then, seems to interfere somewhat with the mechanism by which the pigment of these cells is normally moved.

The *accessory pigment cells* are located in the base of the retina, and send a few processes distad to the outer surfaces of the distal retinular cells, and many proximad through the apertures in the basement membrane to the distal surface of the first optic ganglion. The pigment with which these cells seem to be almost entirely filled is yellowish by transmitted light, and white by reflected light. It is especially remarkable for its powers of reflecting light, and this quality led Exner ('91, p. 97) to designate the layer formed from it by the name of the tapetum. Whether this pigment is influenced by the presence or absence of light is a matter of some uncertainty. Szczawinska ('91, p. 552) states that in Astacus, under the influence of light, the cells containing it enlarge slightly. Exner ('91, p. 105), though at first inclined to regard the accessory cells as influenced by the light, was finally led to abandon this view, and to explain their two apparent conditions by the greater or less degree with which they were covered by the migrating pigment of the proximal retinular cells. In a preparation from an eye kept in the dark, the retinular pigment, as already mentioned, is entirely below the basement membrane, and the accessory pigment is almost entirely exposed, and consequently conspicuous. In the light it is somewhat covered by the black pigment, which under these circumstances fills the bodies of the proximal retinular cells, and it thus becomes less noticeable than before. My own studies on the retina of Astacus (Parker '95, p. 25) led me to agree with Exner that the accessory pigment showed only an apparent change. If, however, any change did occur, it was certainly not an increase in the size (conspicuousness?) of the accessory cells under the action of light, as maintained by Szczawinska, but rather the reverse.

Although in respect to Astacus I am still in doubt as to whether or not the accessory cells show any photomechanical changes, I have not the least hesitancy in stating that in Palæmonetes such a change does occur. The principal difficulty in demonstrating this change comes from the disturbing influence produced by the migration of the pigment in the proximal retinular cells. This difficulty, however, can be overcome by the employment of a depigmenting reagent that will remove the retinular pigment without affecting the accessory pigment. Such a reagent is the depigmenting fluid recommended by Grenacher ('86, p. 214). In preparations representing the dark and the light condition, and depigmented by this means, the differences in the distribution of the pigment in the accessory pigment cells is so striking that no one would question for a moment the photomechanical activities of these cells. In the light (Fig. 1) the accessory pigment forms two concentrations, one in the base of the retina, and the other near the distal surface of the first optic ganglion. These two concentrations are connected by irregular bands of pigment. In the dark (Fig. 2) almost all the accessory pigment is in the base of the retina, the concentration near the ganglion as well as the intermediate pigmented bands being represented by only a few small pigmented patches.

The change from the condition produced by the light to that produced in the dark is indicated in the following steps. After the animal has been about thirty minutes in the dark, the concentration of pigment formerly near the optic ganglion is appreciably nearer the retina. After forty-five minutes, this concentration as such has disappeared, and that in the retina has considerably increased. Finally, after two hours, almost all the accessory pigment lies in the base of the retina, there being only a few small strands proximal to the basement membrane.

In the reverse change under the influence of light, the intermediate pigment strands show a perceptible thickening between ten and fifteen minutes after the eye has been placed in the light, and the full concentration at the level of the ganglion is completed within the period extending from forty-five minutes to an hour after that event.

I have never been able to discover any outlines to the accessory pigment cells except those indicated by the pigment mass itself. Judging from these, the photomechanical changes in the accessory cells involve so radical an alteration in the forms of the cells that the latter may be said to have assumed a different position. In this respect, then, the pigment changes in these cells involve much more active movements than in the case of the proximal retinular cells, and possess something of a locomotor character. So far as I have observed them, they may be compared with perfect propriety to the more or less circumscribed movements of an amœba. When the retina is placed in the light, the cells with their contained pigment creep slowly backward through the apertures in the basement membrane toward the optic ganglion. When the retina is in the dark, they reverse this movement and creep out into the base of the retina. The one particular in which this movement differs from that of an amœba is that of its limitations in direction. Thus the cells always creep either outward or inward. Moreover, in darkness they do not creep indefinitely outward, but after about two hours reach a maximum limit; the same is true of their inward course. These limitations may be due either to the structure of the regions into which the cells creep, or to the intrinsic qualities of the cells themselves; but I have been unable to get conclusive evidence as to which it is.

In the interesting series of eyes of Palæmonetes loaned me by Professor Herrick, the accessory pigment cells of the eyes that had been kept in the dark thirty-eight days presented a condition normal for exposure to the dark. In those eyes that had afterwards been exposed to the light for four hours and three quarters, this pigment had apparently resumed the position normal for exposure to light. The mechanism by which the accessory pigment changes are brought about, unlike that for the proximal retinular pigment changes, is therefore apparently not interfered with by prolonged retention in the dark.

The *distal retinular cells* present photomechanical changes more complex than those in the two kinds of cells already considered. These changes have been described by Exner ('89 and '91), Szczawinska ('91), Herrick ('91), and myself (Parker, '95). All investigators are agreed, I believe, in stating that in the dark these cells occupy a more distal position than in the light. Their probable influence on the amount of effective light that enters the retina led Exner ('91, p. 63) to call them the iris pigment. In Palæmonetes, as I have already shown, there are two distal retinular cells for each ommatidium.

In an animal that has been subjected to the full action of light, the distal retinular cells (Fig. 1, *cl. dst.*) are plump ovoid bodies in contact with the outer ends of the proximal retinular cells. The body of each distal cell has the length of about 30 μ. From its outer end a single process usually extends to, or at least toward, the corneal hypodermis. The whole distal retinular cell, excepting its nucleus and sometimes a portion of its distal process, is filled with black pigment. The whitish pigment that often occurs on the outer surface of these cells represents, as already mentioned, a distal process from the accessory pigment cells.

In animals kept a sufficient time in the dark, the bodies of the distal retinular cells (Figs. 2 and 8, *cl. dst.*) are flattened, and applied to the sides of the cones. They measure about 70 μ in length and possess, in addition to their distal processes, shorter proximal ones, which extend backward to the outer ends of the proximal retinular cells. As before, the cytoplasm is largely filled with black pigment granules, which, however, are often more concentrated in the body of the cell than elsewhere.

It must be obvious from this brief description that in considering the photomechanical changes of the distal retinular cells two factors are to be kept distinct: first, the lengthening and the shortening of the cell body, and, secondly, the distal and the proximal migration of the cell as a whole. That these two elements are distinct can be seen from the fact that in certain insects they are related to each other in a way just the reverse of that which occurs in Palæmonetes; thus, in Lasiocampa, as figured by Exner ('91, Taf. IV. Figs. 28, 29), the distal cells are *short* in their *distal* position, and *long* in their *proximal* one.

The average length of the bodies of the distal retinular cells from the left eye of a given animal prepared in light was about 30 μ. The average length of the corresponding cells from the right eye of the same animal prepared in the dark was about 70 μ. In a series of preparations taken from animals of approximately the same size as that just described, the lengthening of the distal cells in the dark took place at a rate indicated in the first of the following tables.

In a second series the shortening of the cells under the influence of light was shown to take place as indicated in the second table.

The distal and the proximal migration of the cells are difficult to define, because they are accompanied by the lengthening and the shortening of the cells. Taking the nucleus as a fixed point in the cell, the maximum distance of migration is about 50 μ. In the migration from the proximal to the distal extreme, made in the dark, the cell traverses this distance in about two hours. The migration in the reverse direction, under the influence of light, is completed in about one hour and three quarters.

As the cells move outward, their distal processes shorten and their proximal ones form and lengthen. As they move inward, their distal ones elongate and their proximal ones shorten and finally disappear. The rates of these changes, as well as of those given in the preceding paragraphs, are indicated in the following tables of summaries, in which the varying lengths of the parts of the cells are given for successive periods.

Migration in the Distal Direction (in the Dark).

Time.	0 hr.	¼ hr.	½ hr.	¾ hr.	1 hr.	1¼ hr.	1½ hr.	1¾ hr.	2 hr.
Length of distal process .	130[1]	125	110	95	85	65	55	40	30
Length of cell body . . .	30	35	50	55	60	70	70	70	70
Length of proximal process	0	0	0	10	15	25	35	50	60

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[1] All measurements of length are expressed in mikra (thousandths of a millimeter).

Migration in the Proximal Direction (*in the Light*).

Time.	0 hr.	¼ hr.	½ hr.	¾ hr.	1 hr.	1¼ hr.	1½ hr.	1¾ hr.	2 hr.
Length of distal process .	30	35	55	80	100	115	125	130	130
Length of cell body . . .	70	70	65	60	50	40	35	30	30
Length of proximal process	60	55	40	20	10	5	0	0	0

The changes induced in the distal retinular cells by the light are completed, then, in a period between an hour and a half and an hour and three quarters long. The changes that take place in the dark require for their completion from an hour and three quarters to two hours.

Rough estimates of the time necessary for the completion of these changes in different arthropods have been made by various investigators. Szczawinska ('91, p. 552) states that in Astacus the condition characteristic for the dark is reached in six hours, that for the light in two hours. Exner ('91, p. 70) states that in an insect, Lasiocampa, the changes require about half an hour, and Kiesel ('94, p. 105) gives the same time for Plusia. Herrick ('91, p. 455) believes that in Palæmonetes the changes are accomplished in about twenty-five minutes, an estimate that I should regard as rather too low.

Exner ('91, p. 70) has suggested that muscle fibres might be concerned in the migration of the distal retinular cells, an idea that gains some support from the fact that in the eyes of some insects structures like muscle fibres have been seen and described. In the crustacean retina, however, Exner was unable to find anything like muscles. At first sight it might seem probable that what I have described as the proximal and distal processes of the distal retinular cells might be muscular in nature. But the facts that the proximal process disappears entirely during the proximal migration of the cell, and that the distal one seems never to be firmly attached near the periphery of the retina, are opposed to this view. Moreover, in the distal process, which, on the whole, is the more muscle-like of the two, I have been unable to discover any evidence of transverse enlargement in the shortened condition, such as a contracted muscle exhibits. The cell in its distal migration seems to move over the fibre rather than to be drawn onward by a contraction of the fibre. Further evidence against the muscular nature of the motor mechanism of these cells is to be found in the rate at which the movement takes place; 50 μ in two hours is exceptionally slow for the action of any kind of muscle. These observations have led me to conclude that muscular action, as ordinarily understood, has nothing to do with the migration of the distal retinular cells. Obviously, ciliary action is in no way connected with the movements of these cells, and there is left then only amœboid movement as a means of explaining these changes. Each distal cell might be compared to an amœba, which in its migrations outward and inward uses its processes to guide its general motion. The rate and general character of the movement agree well with this explanation. In one respect, however, there is disagreement. Herrick ('91, p. 455), in his account of the action of the distal cells in Palæmonetes, states that, on contracting, these cells fold together somewhat as a ribbon might be folded transversely to its length (cf. Fig. 10), and he believes that, on expanding, they unfold again. This condition is one not easily reconciled with amœboid movement.

Through the kindness of Professor Herrick I have had the privilege of studying his preparations, and I can confirm his statement that in the contracted condition (Figs. 9 and 10) the cells exhibit a series of transverse folds, which are entirely absent from the expanded form. These folds, however, occur, so far as I am aware, only in eyes which have been kept an exceptionally long time in the dark (thirty-eight days in the case of Professor Herrick's specimens), and are then exposed to the light. In my own preparations, none of which had been kept in the dark more than twelve hours, no trace of such folding could be discovered, and I have therefore been led to regard these folds as abnormalities induced by protracted retention in the dark. Notwithstanding this interpretation of the folds, they throw important light, I believe, upon the normal action of the distal retinular cells.

The exact form of these folds is not so simple as might at first be supposed. The body of each cell in its contracted condition consists of an elongated thickened axial portion and two lateral wing-like expansions, each of which terminates in a rather sharp edge. In other words, these distal cells, when contracted, instead of assuming the usual ovoid form, retain more or less the shape that they had when expanded (Fig. 8). In a longitudinal section through the axial portion of the body of one of these cells (Fig. 9) slight folds are observable. In similar sections through the edge of the lateral wings (Fig. 10) the folding is seen to be much more pronounced. The folds are most conspicuous at the edges of the wings, and lose in prominence toward the axial part of the cell. Another peculiarity of these folded cells, as compared with those kept a shorter time in the dark, is that they shorten only to about five sevenths of their original length instead of to three sevenths. Thus their long retention in the dark seems to have prevented a return to the more completely contracted condition normal for the light. The fact that the more peripheral parts of the cells in the contracted condition are the more wrinkled indicates that the axial part has retained its contractile nature more completely than the peripheral parts, and suggests the idea that, since this axis contracts in a definite direction, it must possess something of the nature of a muscular core. It seems to me probable that, whilst the periphery of these cells may be characterized by amœboid movements, the core acts in a more circumscribed way, much as a muscle would. If this is so, the distal and proximal migrations, as well as the expansion of the cell body, are probably manifestations of its amœboid movements, while its shortening is probably due in the main to the muscle-like contraction of its central core. Objection might be raised to this combination of different modes of motion, were it not generally admitted that muscular action is, after all, only a more circumscribed form of amœboid movement.

The presence of a contractile axis in the distal retinular cells is further rendered probable by the fact that in Mysis (Parker, '91, p. 120) an axial core free from pigment has been observed in each distal retinular cell. At the time I first noticed these cores I suspected that they might be the remains of nervous axes, but I now believe there are stronger reasons for suspecting them of being contractile bodies.

The following table gives by way of *summary* the periods required for the completion of the various photomechanical changes in the retina of Palæmonetes.

	From dark to light.	From light to dark.
Proximal retinular cells	$\frac{1}{2}$ hr. to $\frac{3}{4}$ hr.	$\frac{3}{4}$ hr. to 1 hr.
Distal retinular cells	$1\frac{1}{2}$ hr. to $1\frac{3}{4}$ hr.	$1\frac{3}{4}$ hr. to 2 hr.
Accessory pigment cells	$\frac{3}{4}$ hr. to 1 hr.	$1\frac{3}{4}$ hr. to 2 hr.

It is a noteworthy fact, that of these changes those that take place in the light (positive stimulus) are always accomplished more rapidly than the corresponding reversals in the dark. To this statement an apparent exception may be found in the tables on pages 285 and 286, in which are recorded the periods for the contraction and expansion of the distal retinular cells. The body of the distal cell contracts in the light in an interval between 90 and 105 minutes, and expands in the dark in between 60 and 75 minutes, thus apparently accomplishing a change more rapidly in the dark than in the light. The expansion and contraction are, however, not simple operations, but are complicated by the simultaneous production or absorption of the large proximal processes, and it is possible that the discrepancy just pointed out is to be accounted for by this complication.

Before leaving this subject I wish to call attention to the comparative slowness with which all the photomechanical changes of the retina, but particularly those of the distal retinular cells, take place. Exner has shown that the amount of effective light that enters the eye is, in all probability, largely controlled by the action of the distal cells, and has therefore called them the iris pigment. The slowness with which they respond, however, shows clearly that in their action they have little resemblance to the iris of the vertebrate eye, and that their changes correspond only to the more general changes in the amount of light in their surroundings. The name iris pigment seems to me, therefore, somewhat misleading, and hence I prefer to retain the name of distal retinular cells, which indicates at once the present position and the probable origin of these cells, namely, from cells that once formed a part of the retinula itself (Parker, '95, p. 64).

SYMPATHETIC PHOTOMECHANICAL CHANGES.

To ascertain whether the retinas in the two eyes of Palæmonetes were sympathetic toward each other in the same sense that Engelmann believed the retinas in the eyes of vertebrates were, I carried out two sets of experiments, in both of which animals were so placed that one eye was in the dark while the other was exposed to the light. After a sufficient period both eyes were prepared and examined. The two sets of experiments differed only in that I used different means to accomplish the exposure. In one set I tied a living shrimp to the inside of a light-proof box, in which a small hole was made so as to allow one optic stalk of the animal to project into the lighted exterior. Care was taken that the small space between the optic stalk and the edge of the hole should be filled with an opaque material (a mixture of thick Canada balsam and lampblack). After several hours the animal was killed, and its eyes prepared. In the other set of experiments one optic stalk of a living animal was covered with a considerable quantity of the mixture of balsam and lampblack, and, after allowing the animal to swim in a brightly illuminated dish for several hours, it was killed, and both its eyes prepared and examined.

The two sets of experiments yielded essentially the same results, namely, the eyes exposed to the light always presented the condition normal for the light, and those kept in the dark always showed an approach, more or less incomplete, to the condition characteristic for the dark. This incompleteness might be taken as evidence of a partial sympathetic relation between the two retinas; but I believe it is to be explained otherwise. In both sets of experiments the eyes supposed to be blinded were in reality only partially cut off from the light. In the experiment with the light-proof box, I know by actual observation that more or less light made its way *through the optic stalk* that projected outward to the exterior, and thus gained access to the interior of the box. If this is true of the experiment with the box, it is very probable that in the second experiment light passed up through the base of the blinded stalk, and thus reached at least the proximal part of the retina.

These experiments, then, are not wholly conclusive, but, so far as they go, indicate considerable independence in the relations of the two optic stalks. For reasons to be given later, in connection with the experiments on excised stalks, I believe I am justified in concluding that the two retinas are, in reality, wholly independent of each other.

Localized Photomechanical Changes.

Another question that naturally presents itself is, whether different parts of the same retina are sympathetic toward one another, or whether they are entirely independent, i. e. whether or not a retina responds locally to stimulus.

To test this matter, I put minute drops of the mixture of balsam and lampblack on the corneal cuticula of the eyes of several shrimps, and let them swim for a few hours in well illuminated basins. On examining sections of their eyes later, it was found that under each mass of applied pigment the retinal cells showed a condition characteristic for the dark. This was most pronounced in the distal retinular cells, but was also observable in the proximal retinular cells, as well as in the accessory pigment cells. This experiment shows beyond a doubt that the elements of the retina act locally, and respond to differences of light and dark independently of one another. This independence furthermore explains what is not infrequently seen in sections of otherwise normal eyes that have been kept in the dark, namely, occasional single proximal retinular cells which, instead of having their pigment granules transported to the retinal fibres, still hold them in their bodies. Such cells have probably suffered some pathological change by which their individual photomechanical functions have been interfered with. This independence in the action of parts of the retina has already been affirmed by Exner ('91, p. 66) for the compound eyes of insects.

Photomechanical Changes in Excised Eyes and Retinas.

The extent to which the photomechanical changes in the retina are influenced by the central nervous organs has never been determined, I believe, for any arthropod. That some such influence is exerted is implied by several investigators; thus Stefanowska ('90, p. 156) states that, in preparing insects' eyes, she cut the heads of the animals in two so as to prevent the nervous centres from affecting the retinal pigment cells, and Szczawinska ('91, p. 531) recommends as a fixing reagent a hot solution of corrosive sublimate, because the action is so rapid that it is not necessary to use other means of intercepting the central nervous influences. This belief, that the central nervous organs can exert an influence on the retinal pigment cells, is not to my knowledge the result of direct experiment, but is the application to other groups of animals of a generalization first made by Engelmann and his followers for vertebrates. As is well known, Engelmann showed that, when one eye of a frog was protected from the light, the illumination of the other eye, or even of a portion of the surface of the body, sufficed to produce in the pigment cells of the protected eye a condition characteristic for the light. This observation naturally led to the conclusion that the pigment cells of the retina were controlled in their movements by the central nervous organs, and that the optic nerve transmitted impulses centrifugally as well as centripetally. Fick ('95, pp. 77 and 81), however, has recently demonstrated that the same changes occur in a frog's eye even after the optic nerve and sympathetic nerves have been cut, and that therefore the central nervous organs take no part in these changes.

Before turning to the experimental evidence obtained from Palæmonetes, it will be well to consider some of the consequences of this question. In order that the central nervous organs should have any influence on the retinal pigment cells, the two sets of structures must be in nervous connection. So far as is known, the only structures in the retina of

Palæmonetes that have nervous connections are the proximal retinular cells, the accessory cells and the distal cells not being supplied with nerves. Since photomechanical changes occur in both the accessory and the distal cells, the inference might be drawn that in these instances the changes were necessarily independent of the central nervous organs. But it might also be argued that these very changes indicate nervous connections that have escaped the eye of the anatomist. To this it might be replied that, as the nervous connections of the proximal cells are so very obvious, it is highly improbable that the distal and accessory cells have a hitherto undescribed nerve supply. So far, then, as the purely anatomical relations are concerned, they indicate that the photomechanical changes, in the accessory and distal cells at least, are independent of central nervous influences.

In the case of the proximal retinular cells, where each cell possesses a single nerve fibre, the central nervous organs might control the pigment changes. However, if they do, the retinal fibres afford, so far as I know, the first good instance of normal double conduction. Since each retinal nerve fibre is the one nervous process from some proximal retinular cell, and since all these cells show photomechanical changes, it follows that, if these changes are controlled by the central nervous organs, all retinal fibres must transmit central impulses peripherad. As these same fibres are the only nervous connections between the retina and the central nervous organs, some at least must also transmit retinal impulses centrad. Therefore, if it can be shown that the central nervous organs influence the photomechanical changes in the proximal retinular cells, it is likewise demonstrated that double conduction is a natural occurrence. As Fick ('95, p. 73) justly remarks, the solution of this problem involves one of the most fundamental principles concerning the transmission of nervous impulses.

The method by which I proceeded to test this matter in Palæmonetes consisted in examining the changes that went on in eyes after their connection with the central nervous organs had been severed. These connections were conveniently cut in one of two places; either the whole optic stalk was excised, in which case the optic nerve was cut between the brain and the optic ganglia, leaving the latter in normal connection with the retina, or the retinal end of the stalk was cut off, thus separating the retina in the region of the retinal nerve fibres from the optic ganglia as well as from the brain.

To ascertain whether the brain had any influence over the retinal pigment, the following experiments were tried. Four live shrimps, whose eyes were in the condition characteristic for the dark, were decapitated; their right optic stalks were cut off and put in a light moist chamber, and their left stalks, likewise cut off, were placed, as a check on the results of the experiment, in a dark moist chamber. After an interval of two hours both sets of stalks were hardened and afterwards cut and examined. In a corresponding way optic stalks in the condition characteristic for the light were cut off and subjected to the dark.

The results of these experiments are shown in the following tables.

Four Right Optic Stalks in Dark Condition cut off and placed in the Light two Hours.

	Complete change.	Partial change.	No change.
Proximal retinular cells . . .	0	3	1
Distal retinular cells	0	3	1
Accessory cells	0	2	2

The four left optic stalks cut from the same animals and retained, as a check, in a dark chamber, all presented on examination the condition typical for the dark.

Four Right Optic Stalks in Light Condition cut off and placed in the Dark two Hours.

	Complete change.	Partial change.	No change.
Proximal retinular cells . . .	1	3	0
Distal retinular cells	1	3	0
Accessory cells	1	1	2

The four left optic stalks cut from the same animals and retained, as a check, in a light chamber, all presented on examination the condition typical for the light.

It is obvious from these observations that, after the excision of an optic stalk, the photomechanical changes may still take place, if not completely, at least partially, and it might be inferred from this that the brain exerted at least a partial influence over these changes. This conclusion, however, is invalidated by the fact that in one case recorded in the second table the photomechanical changes were carried out *completely*, thus demonstrating that the brain is not in any way essential to these changes. Why this completeness was not seen in other cases I am unable to state positively, though I believe it was owing to the changes that gradually appear in the tissue of the stalk after its severance from the body of the animal. When an optic stalk is excised, the blood in it soon coagulates and other alterations doubtless start up, which finally result in the complete death of the tissues of the stalk. It is these alterations, I believe, that overtake and bring to a standstill the slowly progressing photomechanical movements. But, whatever may be the true explanation of the incompleteness of the changes in excised stalks, the general conclusion remains unaffected, that in Palæmonetes the brain is not essential to the photomechanical changes in the retina.

This conclusion has an important bearing on the question of the sympathetic relations of the two retinas in a given animal. Since the two retinas are nervously connected only through the brain, and since the retinas are not influenced from the brain, it follows that the two retinas cannot be sympathetically related, a conclusion to which observations already recorded have likewise pointed.

If the photomechanical changes are not dependent in any degree on the brain, it may still be asked whether they are not influenced by the optic ganglia. To answer this question, I carried out on excised retinas a series of experiments similar to those just described for the optic stalks. It is much more difficult to separate the retina from the optic ganglia than it is to separate the optic stalk from the brain, but with careful manipulation it can be done, and the following tables give the results of experiments carried out upon such retinas.

Four Right Retinas in Dark Condition cut off and placed in the Light about two Hours.

	Complete change.	Partial change.	No change.
Proximal retinular cells . . .	0	4	0
Distal retinular cells	0	3	1
Accessory cells	0	4	0

The four left retinas kept in the dark as checks on the experiment exhibited the normal condition for the dark.

Four Right Retinas in Light Condition cut off and placed in the Dark about two Hours.

	Complete change.	Partial change.	No change.
Proximal retinular cells . . .	0	2	2
Distal retinular cells	0	4	0
Accessory cells	0	3	1

The four right retinas kept in the light as checks on the experiment exhibited the normal condition for the light.

Although, as the tables show, no case of excised retina with complete photomechanical changes has been observed, several of the cases were so nearly complete that I have no hesitancy in stating that, in my opinion, the photomechanical changes in the retina are as little influenced by the optic ganglia as by the brain.

These experiments, then, lead to two conclusions: first, the brain of Palæmonetes is not essential to the complete photomechanical changes of the retinal pigment cells; and, secondly, the optic ganglia are likewise unessential to these changes. In the latter case, however, the possibility of a slight influence must be admitted. The photomechanical changes of the retinal pigment cells are, in my opinion, induced by the direct influence of the presence or absence of light on these cells. Each cell, then, so far as its mode of action is concerned, is not comparable to a muscle controlled by an efferent nerve, but to a more or less independent organism, which receives a direct stimulus from the exterior, and responds appropriately. The uniformity usually shown by the photomechanical movements in the retina as a whole is to be understood as an individual but uniform reaction of many separate elements to a uniform stimulus. There is nothing in the action of the retinal pigment cells of Palæmonetes that supports the idea of normal double conduction of nervous impulses.

General Summary.

1. The only parts of the retina in Palæmonetes that exhibit photomechanical changes are the three kinds of pigment cells.

2. The proximal retinular cells contain black pigment granules. *In the light* these are scattered more or less uniformly throughout the whole

length of the cell, including the retinal nerve fibre. There are slight concentrations of pigment at the distal end of the cell and around the rhabdome. *In the dark* the pigment is limited to the retinal nerve fibres.

3. The change from the dark condition to the light one is accomplished in from 30 to 45 minutes. The reverse change requires 45 to 60 minutes.

4. These changes are probably due to internal protoplasmic movements, by which the pigment granules in the cells are moved in one or other direction.

5. The accesssory pigment cells contain a yellowish white pigment. *In the light* this is massed partly in the base of the retina, and partly near the distal surface of the first optic ganglion. The two pigment masses are connected by pigmented strands. *In the dark* the pigment is almost entirely in the base of the retina.

6. The change from the dark condition to the light one is accomplished in from 45 to 60 minutes; the reverse change, in from 105 to 120 minutes.

7. These changes are probably produced by amœboid movements of the cells.

8. The distal retinular cells contain black pigment granules. *In the light* they are contracted, and occupy a proximal position in the retina surrounding the axis of the ommatidium near the outer ends of the proximal retinular cells. *In the dark* they are expanded (flattened), and occupy a distal position in the retina, surrounding more or less completely the sides of the cone.

9. The change from the dark condition to the light one is accomplished in from 90 to 105 minutes; the reverse change requires from 105 to 120 minutes.

10. These changes are produced in part by an amœboid movement of the cell, and probably in part by a muscle-like contraction of its axial portion.

11. Each set of photomechanical changes carried out in the light is completed in less time than the corresponding set of reverse changes carried out in the dark.

12. The photomechanical condition of the retina in one eye has no effect upon that in the other eye; i. e. the retinas are not sympathetic.

13. The photomechanical action within the retina is localized, small groups of pigment cells responding to local stimulation.

14. In excised eyes (optic nerve cut), complete photomechanical changes may occur, thus proving that the brain is not essential to these changes.

15. In excised retinas (retinal nerve fibres cut), nearly complete photomechanical changes may occur, thus showing that the optic ganglia are probably not essential to these changes.

16. The incompleteness of the changes in either the excised eyes or excised retinas is probably due to the death of the retinal tissues before the photomechanical changes have been completed.

17. The three kinds of retinal pigment cells probably respond to direct stimulation from without, and are not influenced by nervous impulses from within. There is no good evidence in favor of normal double conduction of nervous impulses.

NOTE.

Since the preceding pages were written, Rosenstadt's ('96) paper on the structure of the compound eyes in Decapods has been published. This contains a brief general account of the migration of the retinal pigment in these crustaceans, and calls for a word of comment. In his description of the directions of motion shown by the pigment under various conditions of light, Rosenstadt agrees with Exner and later investigators, but in his account of how this movement is accomplished he stands entirely alone. His conception of the process can best be put in his own words (Rosenstadt, '96, p. 759): "Beim Uebergange des Lichtauges in ein Dunkelauge gehen mit dem Pigmente volgende Veränderungen vor sich: Das Pigment tritt aus dem vorderen Ende der Retinulazellen [= proximal retinular cells] und wohl auch aus den Retinapigmentzellen [= rudimentary retinular cells] aus. Dasselbe wird von den Fortsätzen der Irispigmentzellen [= distal retinular cells] aufgenommen, die, wie wir gesehen haben, mit dem im Vorderende der Retinulae angesammelten Pigmente im Contact stehen. An diesen Fortsätzen kriecht nun das Pigment hinauf; es findet eine Art Pigmentinfiltration der Irispigmentzellen statt. Gleichzeitig wandert das Pigment nach hinten zu aus den Retinulazellen aus und gelangt hinter die Membrana fenestrata [= basement membrane], wo es von den mit Ausläufern versehenen Zellen aufgenommen wird." This idea that the pigment migrates from one cell to another is, so far as Rosenstadt's account goes, entirely unsupported by direct evidence, and seems to me an unwarranted assumption. The proximal movement of the pigment from the distal end of the retinula to the opposite side of the basement membrane is certainly accomplished within the limits of one set of cells, for, as I have shown in this paper, the pigment even when entirely proximal to the basement membrane lies in the thick retinal nerve fibres, which are merely processes from the proximal retinular cells. Although it cannot be stated with certainty that there is no exchange of pigment between the distal and the proximal retinular cells in Palæmonetes, for in this crustacean in bright light these two kinds of cells are closely applied to each other, it is perfectly certain that in other decapods, as for instance Palæmon, no such exchange is possible; for, as Exner ('91, Taf. V. Fig. 51) has shown, and I can confirm his observations, the pigmented parts of the distal and the proximal retinular cells never touch, even under full light. These reasons, together with the facts set down in the present paper, confirm me in the belief that Rosenstadt's explanation of the migration of the pigment is erroneous, and that the one presented in the foregoing account is correct.

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EXPLANATION OF PLATE.

All the figures were taken from preparations of the eyes of *Palæmonetes vulgaris* Stimp. They were drawn with the aid of an Abbé camera, and are all magnified 335 diameters.

ABBREVIATIONS.

cl. con.	Cone cell.	*fbr. r.*	Retinal nerve fibre.
cl. dst.	Distal retinular cell.	*mb. ba.*	Basement membrane.
cl. px.	Proximal retinular cell.	*nl. con.*	Nucleus of cone cell.
cl. sn.	Accessory pigment cell.	*nl. crn.*	Nucleus of corneal hypodermis cell.
con.	Cone.	*nl. px.*	Nucleus of proximal retinular cell.
crn.	Corneal cuticula.	*rhb.*	Rhabdome.

Fig. 1. Longitudinal section of an ommatidium, showing the arrangement of pigment characteristic for the light.

Fig. 2. Longitudinal section of an ommatidium, showing the arrangement of pigment characteristic for the dark.

Fig. 3. Transverse section of a cone from an ommatidium, such as is shown in Fig. 2 (dark).

Fig. 4. Transverse section through the proximal processes of the distal retinular cells in an ommatidium such as that shown in Fig. 2 (dark).

Fig. 5. Transverse section through the distal retinular cells of an ommatidium such as that shown in Fig. 1 (light).

Fig. 6. Transverse section through the retinula (rhabdome and proximal retinular cells) of an ommatidium like that shown in Fig. 1 (light).

Fig. 7. Transverse section through two groups of retinal nerve fibres.

Fig. 8. Lateral view of a cone with one of its two distal retinular cells still attached. The distal retinular cell shows the condition characteristic for the dark. The preparation was isolated from a retina macerated in Müller's fluid.

Fig. 9. Longitudinal section through the bodies of two distal retinular cells, which show slight foldings accompanying their shortening. The preparation was made from an animal which had been kept in the dark thirty-eight days and then exposed to light for four hours and three quarters. The figure was drawn from preparations made by Professor F. H. Herrick, who kindly granted the author the privilege of studying them and making drawings from them.

Fig. 10. Longitudinal section through the edges of two distal retinular cells (see p. 287), from the same set of sections as that from which Fig. 9 was drawn.

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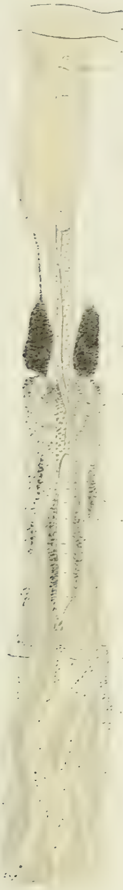
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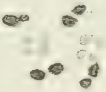

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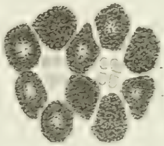

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BULLETIN

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CONTENTS.

PAGE

No. 1. — Contributions from the Zoölogical Laboratory. LXXXIII. Contributions to the MORPHOLOGY of the TURBELLARIA. II. On some TURBELLARIA from Illinois. By W. McM. WOODWORTH. (1 Plate.) October, 1897 1

No. 2. — On the Relations of certain PLATES in the DINICHTHYIDS, with Descriptions of New Species. By C. R. EASTMAN. (5 Plates.) October, 1897 17

No. 3. — Contributions from the Zoölogical Laboratory. LXXXIV. TRICHONYMPHA, and other PARASITES of TERMES FLAVIPES. By J. F. PORTER. (6 Plates.) October, 1897 45

No. 4. — Contributions from the Zoölogical Laboratory. LXXXV. Variations in the BRACHIAL and LUMBRO-SACRAL PLEXI of NECTURUS MACULOSUS RAFINESQUE. By F. C. WAITE. (2 Plates.) November, 1897 . . . 69

No. 5. — Reports on the Dredging Operations in the "Albatross" in 1891. XXII. The ISOPODA. By H. J. HANSEN. (6 Plates and Chart.) December, 1897 93

No. 6. — Contributions from the Zoölogical Laboratory. LXXXVII. The Thoracic Derivatives in the POSTCARDINAL VEINS in SWINE. By G. H. PARKER and C. H. TOZIER. March, 1898 131

No. 7. — Contributions from the Zoölogical Laboratory. LXXXIX. The SEGMENTATION of the NERVOUS SYSTEM in SQUALUS ACANTHIAS. A Contribution to the MORPHOLOGY of the VERTEBRATE HEAD. By H. V. NEAL. (9 Plates.) May, 1898 145

No. 1. — *Contributions to the Morphology of the Turbellaria.*

II.

On some Turbellaria from Illinois.[1] By W. McM. Woodworth.

The material upon which this paper is based was collected by the staff of the Biological Experiment Station of the Illinois State Laboratory of Natural History at Havana, Illinois, and came from the Illinois River and the streams and lakes tributary to it.[2] The material was collected between the first of July and the last of October, 1894, and the first of March and the last of September, 1895. I am indebted to Prof. S. A. Forbes, Director of the Illinois State Laboratory, for the privilege of studying the collections, and am under obligations to Dr. C. A. Kofoid, Superintendent of the Experiment Station, and to Prof. Frank Smith for their patience and kindness in answering my many inquiries, and for sending me living material from time to time. I must thank these gentlemen also for the excellent state of preservation of all the material that came into my hands.

Although I have to report but two species that are probably new, it is hoped that these pages will help to clear away some of the confusion that exists in the published accounts of the North American fresh-water Turbellaria. Although the figures accompanying this paper do not, with two exceptions, represent new forms, they are, I believe, the first published illustrations, in the natural colors of the living animals, of some of our common fresh-water Turbellaria.

I have not entered into the finer anatomy of the species to any extent, as that would have been beyond the scope of the paper. Unfortunately, too, not all of the species were represented by sexually mature individuals, and as the characters of the sexual organs are of the highest systematic importance, the unavoidable lack of data upon this subject must necessarily leave my work more or less incomplete. It is to be regretted also that living material could not be had of all the species treated of, as descriptions based solely upon alcoholic material are, to say the least, unsatisfactory, owing especially to the effect of reagents upon the pigments.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXXIII.

[2] For a description of the localities under investigation by the Experiment Station, see C. A. Hart, On the Entomology of the Illinois River and adjacent Waters. Bull. Ill. State Lab. Nat. Hist., Vol. IV. p. 150, 1895.

The collections comprise five (?) species of Triclads and two Rhabdocœls. Three of these I hope to show are cosmopolitan in their distribution.

Dendrocœlum lacteum OERSTED.

Figures 1, 9–15.

Dendrocœlum lacteum OERSTED, 1844, p. 52. WOODWORTH, 1896^{b}, p. 1048.

Dendrocœlum superbum GIRARD, 1851, p. 265; 1851^{a}, p. 2.

Dendrocœlum superbum LEIDY (non Girard), 1852^{b}, p. 288.

Dendrocœlum pulcherrimum GIRARD, 1851, p. 265; 1851^{a}, p. 2.

Procotyla fluviatilis STIMPSON (Leidy MS.), 1857, p. 23. DIESING, 1862, p. 517. LEIDY, 1885, p. 51. HALLEZ, 1890, p. 105. GIRARD, 1893, p. 164. WOODWORTH, 1896, p. 95; 1896^{a}, p. 241.[1]

Procotyla leidyii GIRARD, 1893, p. 166.

Station C; 13,166, "small pool on sandy margin of Thompson's Lake near Station G."

Color, milk white; creamy, yellowish, or, in larger, older specimens, roseate; no pigment except in eye-spots. Very translucent; intestine in all its ramifications easily seen, grayish to brown or black according to the character of the contents, more deeply colored in larger specimens. A slight constriction immediately behind the plane of the eyes, marking off an anterior head end and producing the lateral projecting rounded cephalic appendages. Gradually widening posteriorly from constricted or neck region to a point about one sixth the total length from the anterior end, then margins are parallel to about one fifth the distance from the posterior end, tapering gradually from this point to the rounded posterior extremity. When in active motion and fully extended, the lateral margins are smooth and nearly parallel; but when partly contracted or at rest, the margins are very sinuous or crenate and thrown into folds, like the margins of many marine Planarians. A well marked median adhesive disk or sucker at the anterior end, the diameter of which is about one third the broadest diameter of the head. When the animal is in motion the shape of the anterior end is continually changing, owing to the protrusive and retractive movements of the disk, which can be protruded for a considerable distance, though projecting only slightly when in the retracted condition. Eyes usually two, but frequently accessory eye-spots from one to six in number. Distance between the eyes a little greater than from eyes to margin of head. Mouth opening (in preserved material) slightly posterior to a point midway between anterior and posterior ends. Gonopore (in preserved material) two sevenths of the total length from the posterior end. Length from 10 to 22 mm.; greatest breadth from 2 to 3 mm.

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[1] By a gross error I have in the above paper also referred to Keller und Tiedemann's Nordamerik. Monatsber. for 1851.

Dendrocœlum lacteum, which is one of the commonest and most widely distributed of European fresh-water Planarians, has often been the object of study, and its structure is better known, perhaps, than that of any other Triclad. Chief among the papers dealing with this species is that of Iijima (1884); our American form agrees so closely with his account that a discussion of the finer anatomy of the species will not be entered into here, except in so far as regards the anterior adhesive disk, and some points in connection with the male sexual organs; for other details the reader is referred to Iijima.

It is remarkable that Iijima should have overlooked the adhesive disk of *D. lacteum*. Though he states (p. 362) that he did not find the organ, two of his Figures (Taf. XXII. Figs. 9 and 10) are very suggestive, and coincide with similar preparations of my own. The organ was seen by von Baer (1827, p. 715), who describes it as a "kleine Pupille"; Dugès (1828, p. 150) also speaks of it as "un renflement qui peut aisément se creuser en cupule, en ventouse semblable à celle de la queue des sangsues et la face inférieure des Douves," and he shows it in his Fig. 7, Pl. 4. Leydig (1864) figures it (Taf. I. Fig. 2), and in his account of its structure mentions the absence of rhabditi and cilia in the cells lining the depression. The organ is characteristic of the genus Dendrocœlum, and occurs in every other species of the genus whose structure has been investigated. The failure of Iijima to find the organ is explained by Weltner (1887, p. 800) as being due to the great variability of the organ itself in the same individual, depending upon different phases of contraction and expansion, it being at times difficult to recognize it. The variability in the shape of the disk was also referred to by Leydig (*loc. cit.*), and Girard (1893, Pl. 4) figures many phases of its activity. I also can testify to the great mobility of the adhesive organ, and to its varying prominence in the same and in different individuals.

As a rule, it is more prominent in the largest, oldest individuals; in those 10 mm. and under in length, I have often had considerable difficulty in recognizing it even in sections, there being nothing to replace it but a shallow groove. Figures 13–15 are from sections of an individual of the largest size, and represent the organ in an exceptionally prominent condition. The organ cannot be compared to the sucker of cotyligerous Turbellaria, or to the muscular sucking disks of other Platyhelminths, nor to that of the leech; it lacks the special musculature often so elaborately developed in these. It is simply a depression at the anterior end of the animal into which open the numerous mucous glands which in most Triclads are found in this region. It is comparable, rather, to the frontal organ of the Acœla, and more particularly to the organ existing at the anterior end of *Mesostoma lingua*, which has been described and figured by Graff (1882, p. 288). In this species the pit is formed by the inversion of that part of the anterior end where the two great tracts of rhabditi ("Stäbchenstrassen") open to the exterior, and according to Graff is not permanent or constant. I have elsewhere (1891, p. 23) expressed my belief in the homology of the "Stäbchenstrassen" of the Rhabdocœls with the cephalic slime glands of Triclads, and a comparison of the sagittal section of *M. lingua* (Graff, 1882, Taf. VI. Fig. 3) with Figure 15 of this paper is strikingly suggestive in this regard. Kennel (1888, p. 455) has also shown that in many fresh-water Triclads there appears in preserved material a more or less shallow groove, or depression, on the ventral surface at the anterior end corresponding to a region by which the living animals are able to attach themselves. It is the region where the cephalic slime glands open to the exterior. He suggests for the ridges at the sides of these ventral depressions the names "Haftwulsten" and "Haftlappen." Grube (1872) has also described similar pits or grooves in several fresh-water Planarians.

The organ in *D. lacteum* is not a true sucker, nor does the animal employ its anterior end for the purposes of attachment to any greater degree than the posterior or lateral margins of its body, along the ventral surface of which numerous mucous glands have their openings. In truth, it is the margins and posterior end that adhere more firmly to a support ; often when the animal is forcibly removed from the side of the aquarium the parts of the margin or the posterior end will adhere so firmly to the glass that the points of attachment are drawn out into digitate processes. Figures 13 and 14 are from transverse sections through the adhesive pit of *D. lacteum*, Figure 13 being through the almost extreme anterior part, while Figure 14 is somewhat more posterior. Both sections are from the same individual, — one in which the organ was unusually well developed. Figure 15 represents a sagittal section through another individual, and Figure 9 is a surface drawing of an individual killed in hot corrosive sublimate. It will be seen that the region involved in the organ embraces all that portion of the hypodermis occupied by the openings of the mucous glands. As already shown by Leydig (1864), the hypodermis which lines the depression is devoid of cilia and rhabditi, the latter being replaced by the mucous glands, and the transition from one to the other being gradual. The exact histological character of the hypodermis lining the depression could not be ascertained, the terminal ducts of the glands being so closely compacted as to mask all details in this region. In Figures 14 and 15 are seen cross and longitudinal sections of the retractor muscle of the organ. Nothing in the shape of a protractor muscle could be discovered, this function possibly being assumed by the circular muscles of the dermo-muscular sac.

The variation in the number of the eye-spots is not a feature peculiar to the American form of *D. lacteum*, as I stated in a previous note (1896^b, p. 1048), for accessory eyes, "Nebenaugen," have been observed in this species by Carrière (1882, p. 164) and Iijima (1884, p. 438), according to whom they are not rare. According to my observations there is in such cases usually one pair of eye-spots, corresponding to the normal single pair, which is more prominent than the accessory eye-spots. In what appears to be a closely allied form, *Sorocelis gutata* Grube (1872), there exist two series of eye-spots arranged in the form of two arcs ; the number of eyes in each arc is usually seven, but there may be as few as two, nor is the number always the same on both sides. I have never observed more than a total of eight eye-spots in *D. lacteum*, there being from one to six accessory eyes, either equally or unequally distributed on the two sides of the head. Girard (1893, p. 165) describes and figures variations in the number of the eyes, and also shows the accessory eyes to be smaller than the pair of normal eye-spots. Leidy (1885, p. 50) also speaks of the accessory eyes. Of the many Illinois specimens of *D. lacteum* that have come under my observation, 33 per cent of the individuals exhibited variations in the number of the eyes.

Anastomoses in the branches of the intestine exist in most of the specimens examined; these are usually confined to the branches of the posterior trunks, which are often united by transverse commissures. In one case there were three such transverse commissures. Girard (1893, Pl. 4) figures an individual in which the posterior trunks can no longer be recognized as such, the digestive tract existing as a meshwork or reticulum. Leidy (1885, p. 50) and Iijima (1884, p. 390) also mention anastomoses, and the latter figures a commissure uniting the posterior trunks, while Wheeler (1894, p. 176), in a species which he believed to be *D. lacteum*, failed to detect any such connections. Hallez (1892) also figures such connections for this species.

I have little to add to the account of the sexual organs given by Iijima, but do not find the penis to be so nearly spherical in shape as that figured by him. The shape of the male organ is more like that figured for *D. lacteum* by Schmidt (1861, Taf. IV.), longer and more cylindrical. Nor is the cavity of the penis so large as that figured by Iijima, the muscular walls being much thicker (Figs. 10–12). The cavity of the penis is lined with a glandular epithelium, which projects into the lumen of the organ in folds, thus producing a large secreting surface. It is possible, of course, that the cavity varies at different periods of sexual activity. In one important particular only do my observations on the sexual organs differ from those of Iijima. According to that author the vasa deferentia open separately and directly into the cavity of the penis and at considerable distance from each other. My observations do not confirm the existence of such conditions, but show that the vasa deferentia unite into a slender ductus ejaculatorius, which extends in the longitudinal muscles of the organ along its ventral surface to that point where the penis begins to taper off to form the slender distal free intromittent part of the organ (Fig. 10). At this point, which may be designated as the root of the penis proper, and corresponds with the posterior limit of the glandular cavity, the duct becomes confluent with the cavity of the penis. In other words, the glandular cavity of the penis may be said to pour its secretions at this point into the seminal duct, and the greater mass of the penis can be compared to a prostate gland, the Körnerdrüse of Polyclads. In transverse section it is often difficult to follow the course of the duct, owing to its small size and to the fact that the lumen is often obliterated by the approximation of its walls, and frequently lies in one of the glandular folds projecting into the cavity of the organ (Fig. 12). The sheath of the penis in its deeper portions is thrown into many folds to provide a greater surface for the glands that secrete the shell of the cocoon (Fig. 11). These glands are spoken of by Iijima, but are not figured by him.

In a recent paper I (1896^b, p. 1048) have discussed the synonymy of Leidy's *Procotyla fluviatilis* and expressed my belief in the identity of this species with *Dendrocœlum lacteum*; upon the evidence presented above, I wish to emphasize my conviction in this regard. The apparent differences between the forms are in the American form the possible greater prominence of the frontal adhesive organ, the more frequent variation in the number of the eyes, and the separation of the seminal duct from the glandular part of the male sexual organ. The first two of these differences, as I have endeavored to show, are differences in degree only, and have no systematic value. The discrepancy between my account of the male sexual organs and that of Iijima alone stands as a real difference. Although I can find no account of anything similar in other Triclads, there are conditions comparable to these in the male organs of Polyclads and Rhabdocœls (Lang, 1884, and Graff, 1882), and it is possible that this detail has hitherto been overlooked in Triclads.

Neither have I any hesitancy in placing under *D. lacteum* Girard's *D. pulcherrimum* and *D. superbum*. The former differs, he says (1851, p. 265), from *D. lacteum* "by having three pairs of eyes instead of two," while his *D. superbum* (1851^a, p. 2) "gleicht vielleicht noch mehr als die vorgehende Art [*D. pulcherrimum*] den *D. lacteum*, wovon es sich unterscheidet durch kleinere dünnere Gestalt, zwei Paar Augen, vorstehendere Hörner und rothe oder milch weiss Farbe." It is significant, too, that Leidy (1852^b, p. 288) should have first ascribed his *Procotyla fluviatilis* to Girard's *D. superbum* (see Woodworth, 1896^b, p. 1048), and that Girard, in his recent extended monograph of North American Turbellaria, makes no mention of these two old species of his.

Planaria gonocephala Dugès.

Figure 5.

Planaria gonocephala Dugès, 1830, p. 83.

Planaria gonocephaloides Stimpson, 1857, p. 23. Diesing, 1862, p. 498. Silliman, 1885, p. 69.

Dugesia gonocephaloides Girard, 1851, p. 265; 1851^a, p. 2; 1891, p. 183.

Sides parallel, tapering gradually posteriorly to a rounded point. Anterior end obtusely pointed, angular, the sides of the head making an angle of about 60°. Two angular cephalic appendages. In alcoholic material the auricles are not prominent, scarcely showing at all in some specimens. Length of head about $\frac{1}{10}$ of the total length of the animal. Eyes two, in a plane joining the apices of the auricles. Clear area surrounding the eyes sometimes elongated in the antero-posterior direction. Color, dark reddish brown to grayish brown, uniform. Posterior margins of auricular appendages free from pigment. Length 9 to 15 mm., greatest breadth $\frac{1}{2}$ to 2 mm. (Two alcoholic specimens, which must have measured 20 mm. or more in length when alive.)

11,664*b*, Station C; 13,069, Station C.

Only one of the specimens exhibited sexual organs. There is no copulatory bursa and the oviducts open separately into the vagina immediately before it enters the genital atrium. The species in every way agrees with descriptions of the European form. There can be no doubt that it is the species described by Girard as *Dugesia gonocephaloides*. According to this author the latter differs from *P. gonocephala* only in the elongated form of the clear areas surrounding the eye-spots, and upon this meagre difference is founded the genus which Girard afterwards (1891) extended to include all forms bearing angular cephalic appendages. Stimpson and Diesing retained the specific name, but placed it under the genus Planaria, a fact that was apparently unknown to Silliman, who renamed it *Planaria gonocephaloides*. Hallez (1890, p. 78) has discussed the value of Girard's genus Dugesia, and places *D. gonocephala* as a synonym of *P. gonocephala*, in which species the elongated shape of the periocular areas is not uncommon. *P. gonocephala* has been shown by Iijima (1890, p. 338) to be cosmopolitan in its distribution, as it was found by him in Japan.

The color of the American representatives of *P. gonocephala* differs from that of the European in being of a deeper hue. The European forms vary from a gray to a brownish green, while the Illinois specimens are of a deep brown, which is well reproduced in Figure 5. Some specimens from France that I have received through the kindness of Professor Hallez, of Lille, are almost white in the alcoholic condition. Girard (1893, p. 183) describes the color of *Dugesia gonocephaloides* as often being a blackish brown.

Planaria dorotocephala, sp. nov.

Figures 4, 7.

Planaria maculata var. *a* GIRARD, 1893, p. 182.

Sides parallel, tapering gradually to a point posteriorly. Anterior end large, sharply pointed, the sides of the head making an angle of about 45° with each other. Two long sharply pointed, very prominent auricular appendages, slightly posterior to the plane occupied by the eyes. Auricles always prominent in preserved material. Length of head about $\frac{1}{6}$ of the total length of the animal. Width of the head at its junction with the auricular appendages greater than the diameter of body anywhere posterior to the appendages. Color, reddish to yellowish brown, uniform. Posterior margins of auricular appendages free from pigment. Occasionally a narrow light median streak extending caudad from just back of the eye-spots. Length 8 to 13 mm., greatest breadth $\frac{1}{2}$ to $1\frac{1}{2}$ mm.

22,081; Station H, Matanzas Lake; Station C; Havana.

A very active, restless, rampant form. When in motion the head is elevated and moved from side to side, the long auricular appendages being elevated above the head. After being disturbed, it does not come to rest for a long time as compared with *P. gonocephala* and *P. maculata*, the latter being particularly sluggish. A peculiarity of this species is the frequent occurrence of accessory posterior intestinal trunks, a condition that was present in fifty out of seventy-one specimens examined. In place of the two posterior trunks of the intestine, which exist in the ordinary Triclad type, there are often as many as three parallel trunks on each side of the pharyngeal chamber (Fig. 7). The accessory trunks either take their origin at the root of the pharynx, like the two normal posterior trunks, or exist as parallel branches of the latter, and usually unite with it and with each other close to their posterior terminations. I have never seen any anastomoses of the trunks of one side of the body with those of the other side, as in *D. lacteum.* When accessory trunks are present, they bear no lateral branches, but in place of these possess slight projections or buds, the lateral branches probably being suppressed through lack of space. The anterior portion of the intestinal tract, in almost every case where the specimens were not too heavily pigmented to be studied, exhibited anastomoses of the lateral branches, the intestine in some instances existing as a network (Fig. 7). (See under *D. lacteum*, *ante*, p. 2.) Unfortunately, I can say nothing in regard to the sexual organs of this species. In over one hundred individuals examined, not one was sexually mature or showed any signs of sexual organs.

Girard (1893, p. 181) describes three varieties of *Dugesia maculata.* The description he gives of his first variety, var. *a*, agrees closely with the form described above in size and shape, in color, in the frequent occurrence of the light median streak, in the greater length of the auricular appendages, and the more pointed shape of these and the head end. His Figure 56 also shows a third posterior trunk of the intestine, but median in position and anastomosing with the lateral trunks. There can be little doubt that var. *a* of Girard's *D. maculata* and *P. dorotocephala* are the same.

There is also a striking resemblance between *P. dorotocephala* and Kennel's figure of *P. aurita* (1888, Fig. 3).

Planaria maculata Leidy.

Figures 2, 3.

Planaria maculata Leidy, 1848, p. 251; 1848^a, p. 78; 1852, p. 225; 1852^b, p. 289; 1885, p. 50. Diesing, 1850, Vol. I. p. 205; 1862, p. 499. Stimpson, 1857, p. 23. Silliman, 1885, p. 70. Woodworth, 1896, p. 94; 1896^a, p. 240.
Dugesia maculata Girard, 1851, p. 264; 1851^a, p. 2; 1893, p. 181, var. *b* and *c*.
Planaria tigrina Girard, 1851, p. 264; 1851^a, p. 2; 1891, p. 179.

Anterior end pointed, sides of the head making an angle of about 60°. Two angular cephalic appendages. Length of head about $\frac{1}{10}$ the total length of the animal. Eyes two. Sides parallel to about $\frac{2}{3}$ of the total length from the anterior end, then tapering gradually to a rounded point. Color, blackish to purplish by reflected light; blackish or gray by transmitted light. In smaller young specimens, the pigment occurs in isolated patches and spots; in older specimens the pigment patches become more confluent, chiefly in the median region leaving clear irregular areas scattered over the surface of the animal.

Smaller spots of deep brown or black occur scattered over the surface among the larger patches. In the largest, oldest specimens there are very few or none of the clear areas. Frequently a light median streak more or less free from pigment occurs, extending backward from between the eye-spots (Fig. 3). Length 4 to 9 mm., greatest breadth $\frac{1}{2}$ to $1\frac{1}{2}$ mm.

Station D ; 13,011, Station C ; 13,113, Illinois R. at Havana ; 22,050*a*, Station E ; 13,521, Station L ; 22,020, Station K ; 22,033*d*, Station L ; 22,011*c*, Station L ; 22,053, Station H.

Planaria maculata is the commonest of our fresh-water Planarians and was the first one to be described (Leidy, 1848) ; however, nothing has been published regarding its sexual organs, and I am unable to offer anything in this regard ; not one of the hundreds of specimens that came under my observation was sexually mature. The species, as already mentioned, is sluggish, seldom being in motion in the aquaria, and when stirred up in company with *P. gonocephala* and *P. dorotocephala* it is the first to come to rest. It is possible, as also suggested by Leidy (1885, p. 50), that it is nocturnal in its habits. It is usually found on the protected sides of stones, of empty Unio shells, or of aquatic plants, and often huddled together in large numbers.

About 40% of the Illinois individuals that I examined exhibited mutilations at the anterior or posterior ends, either by the absence of a head, or by being truncated posteriorly. In the cases where the posterior end is lacking the pharynx, instead of occupying a position midway between the anterior and posterior ends, extends almost to the posterior limits of the animal. There is no pigmentation about such scars. I have elsewhere (1896^a, p. 240) referred to the mutilations in *Planaria maculata*, and suggested that they were the result of reproduction by transverse division. I have since learned from Dr. Harriet Randolph that the species divides spontaneously, and that small fragments from any part of the body will regenerate into a new worm.[1]

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[1] Through the courtesy of Dr. Randolph I am able to present the following table. The material upon which the experiments were made was collected on the island of Naushon, Vineyard Sound, Mass.

PLANARIA MACULATA. CASES OF FISSION.

Specimen.	Date of Isolation.	Kind of Water.	Date of First Fission.	Interval.	Date of Second Fission.
1	July 24	Rain	July 30		
2	July 24	Rain	August 1		
3	July 24 (?)	Rain	August 3	14 days	August 17
4	August 17 *	Lake †	August 21		
5	August 17 (?)	Lake †	August 25		
6	August 18	Spring	August 20		
7	August 17 or 18	Spring	August 26		
8	August 17 or 18	Spring	August 28		

* Whole number isolated on August 17 and 18 was forty individuals.

† From which the Planarians came.

Van Duyne (1896) experimented with a form which he states "war die *Planaria torva* von Wood's Holl." A study of his figures leads me to believe that the species used by him was *P. maculata.* I have found *P. maculata* to be very common at Wood's Holl and elsewhere on Cape Cod, where I have collected and where I have never met with a species that resembles in any way the *P. torva* of Europe ; nor has that species ever been described from the United States. In *P. torva* the head is not defined from the body by lateral cephalic appendages, the anterior end of the animal is simply rounded. The contrary is true of the species shown in Van Duyne's figures, where there is indicated a sharply marked angular head and well marked projecting cephalic appendages.

Many of the specimens showed dark spheroidal bodies scattered through the parenchyma, as many as fifteen of the bodies occurring in a single individual. In sections they proved to be small encysted Trematodes. The cysts measured from 0.025 to 1.1 mm. in diameter. I have also met with Trematodes in the mesenchyma of *Bdelloura parasitica.*

Borelli (1895) has called attention to the resemblance of his Paraguayan *P. dubia* to our *P. maculata* as described by Girard, and has named a variety of it *P. dubia* var. *maculata.*

Planaria unionicola, sp. nov.

Figure 8.

It is with considerable reserve that I offer a new species upon the meagre evidence at my disposal, but such data as there are cannot be reconciled with descriptions of any known species. There was but one specimen (13,646), which was much contracted and shrivelled. It was found creeping on the mantle of *Unio alatus,* dredged from deep water in the Illinois River near Havana, August 30, 1895. According to the collector's notes the general color of the animal was "brownish red . . . mottled with purplish dots." On an outline drawing evidently made from the living animal, and which is reproduced in Figure 8, the color is also indicated as "light brick red" and the "purple dots" as occurring "all over the surface in masses, except at the margins," the dotted line in the figure no doubt representing the limits. The red color is also noted as being absent over an elongated posterior median area extending nearly to the posterior end of the animal (Fig. 8). The head end has a sinuous outline, producing three lobes or rounded projections, a median anterior one and two lateral cephalic appendages. There are two eyes occupying the inner margins of large circular periocular spaces. The sides are nearly parallel, and the posterior end is abruptly rounded, so blunt, indeed, as to suggest an injury or that transverse division had taken place. If the clear median elongated space indicates the position of the pharynx, its extreme posterior position is also indicative of an injury or a division. The color of the alcoholic specimen was a deep rusty red. Owing to the crumpled condition of the specimen nothing of any internal organs could be recognized, even when subjected to the most powerful clearing reagents. The length of the specimen was 2.8 mm., the greatest breadth 1.8 mm. When alive the worm probably must have attained a length of from 8 to 10 mm.

Whether the occurrence of the animal on the mantle of Unio is an indication of a parasitic mode of life, like that of the Triclads of the genera Bdelloura (Leidy, 1852[a]) and Syncœlidium (Wheeler, 1894), or whether its occurrence was purely accidental, can only be determined by careful and extended search.

Mesostoma ehrenbergii O. Schmidt.

Figure 6.

Mesostoma ehrenbergii O. Schmidt, 1848, p. 47.
Mesostoma wardii Woodworth, 1896, p. 95; 1896[a], p. 241.

No. 13,521, Station L; No. 13,626, Illinois River.

In a report on the Turbellaria collected by the Michigan Fish Commission I (1896, 1896[a]) described what I believed to be a new species of Mesostoma under the name of *M. wardii*, basing the species chiefly upon the uniformly small size and the absence of cephalic tracts of rhabditi or "Stäbchenstrassen." A comparison, however, with a larger number of Illinois Mesostoma has convinced me of the identity of both the Michigan and Illinois forms with *M. ehrenbergii* of Europe, and I must hereby cancel the species established by me in 1896. The Illinois specimens range from 1½ mm. to 6 mm. in length, while the Michigan specimens measured only from 2 to 3 mm. In all of the small Illinois specimens the cephalic tracts of rhabditi are lacking, and are prominent only in the largest individuals. The largest of the specimens, 6 mm. in length, contained eight young worms in the left uterus, the right uterus being empty.

The viviparity of *M. ehrenbergii* was known to Focke (1836), and the same author has described the differences between the brown hard-shelled winter eggs and the smaller translucent summer eggs, and pointed out the fact that in the viviparous condition the young ones arise from the thin-shelled summer eggs. The simultaneous occurrence of both summer and winter eggs in the same individual was observed by Leuckart (1852). Four of the Illinois specimens contained the characteristic large opaque brown hard-shelled winter eggs, and therefore agree with the European form in producing both kinds of eggs at the same season, though in no case were there both kinds of eggs actually present in the same individual. About 40% of the individuals contained the translucent summer eggs, the smaller specimens showing no signs of sexual organs. The winter eggs have the same shape as those of the European species, such as would result if one half of a hollow sphere were infolded into the other half. As in the European species, too, the diameter of the winter eggs considerably exceeds that of the summer eggs, the former measuring 0.525 and the latter 0.350 mm. in diameter. The occurrence of *M. ehrenbergii* in the United States also gives to this well known species a cosmopolitan distribution.

Stenostoma leucops O. Schmidt.

Stenostoma leucops O. Schmidt, 1848, p. 59; Silliman, 1885, p. 55; Ott, 1892.
Stenostoma neoboracense Girard, 1893, p. 220.

Said to have been abundant in the aquaria of the laboratory during May, 1896. Of this species I received only some stained mounted specimens. The following account is from notes made by Dr. Kofoid upon living material.

When extended, in motion, the worms measured 1 to 1½ mm. in length. Margins transparent, central portion brownish, posterior third of the animal often with a faint tinge of pink or maroon, and in one specimen this color extended throughout the length of the animal. Several lobe-like projections on the surface near the mouth when the animal is contracted. The anterior end, when extended, exhibits two lateral depressions, — the ciliated pits. The projecting anterior end is very mobile, and from its activity undoubtedly highly sensitive. No trace of sexual organs. Cilia very prominent on the general surface of the body, and always directed forward when the animal is quiescent. Locomotion is sometimes in a posterior direction, and is accompanied by waves of constriction progressing from in front backwards. Forward motion, however, is apparently due wholly to ciliary action. Reproduction by fission was indicated in some specimens by the existence of well marked constrictions at about one third the total length from the posterior end; the constriction involved both the hypodermis and the digestive tract.

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EXPLANATION OF THE PLATE.

ABBREVIATIONS.

brs.	Copulatory bursa.	*ov'dt.*	Oviduct.
dt. ej.	Ductus ejaculatorius.	*pe.*	Penis.
gl. sh.	Shell gland.	*ut.*	Uterus.
gl. pr'st.	Prostate gland.	*va. df.*	Vas deferens.
go'po.	Gonopore.	*vag.*	Vagina.
mu. ret.	Retractor muscle.	*x.*	Vesiculæ seminales.

The lines adjacent to the Figures 1, 2, and 4–7 indicate the natural size of the object.

Fig. 1. Dendrocœlum lacteum. From life, × 4.

Fig. 2. Planaria maculata. From life, × 6.

Fig. 3. P. maculata. Head end, to show the occurrence of the light median streak. From life.

Fig. 4. Planaria dorotocephala, sp. nov. From life, × 7. The line at the left of the figure indicates the natural size of the colored part of the figure only.

Fig. 5. Planaria gonocephala. From life, × 5.

Fig. 6. Mesostoma ehrenbergii, showing young worms in the left uterus. From a specimen in clove oil, × 14.

Fig. 7. P. dorotocephala, sp. nov., to show intestinal tract. A reconstruction from a series of frontal sections, × 6.

Fig. 8. Planaria unionicola, sp. nov. From a drawing, apparently from life, accompanying the specimen.

Fig. 9. D. lacteum. Head end, to show the adhesive organ. From an alcoholic specimen killed in corrosive sublimate, × 5.

Fig. 10. D. lacteum. Diagram of sexual organs, × 20.

Fig. 11. D. lacteum. Longitudinal section to show the sexual organs, × 50.

Fig. 12. D. lacteum. Transverse section through penis, × 40.

Fig. 13. D. lacteum. Transverse section through extreme anterior end, to show the adhesive organ, × 80.

Fig. 14. D. lacteum. Transverse section from same individual as last, somewhat posterior to it, × 80.

Fig. 15. D. lacteum. Median longitudinal section through the anterior end and adhesive organ, × 80.

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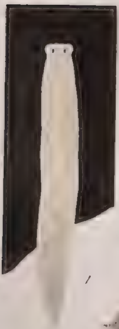
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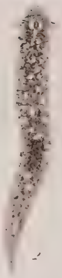
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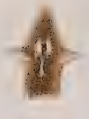
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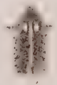
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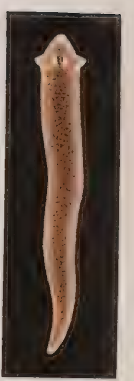
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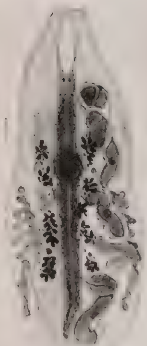
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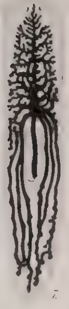
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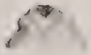
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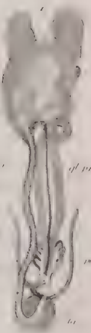
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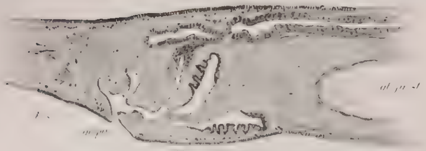
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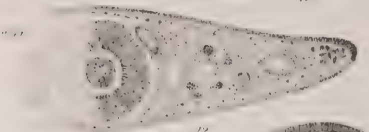
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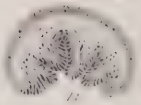
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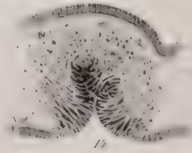
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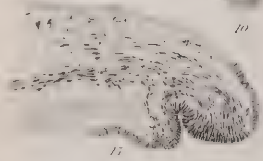
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No. 2. — *On the Relations of Certain Plates in the Dinichthyids, with Descriptions of New Species.* By C. R. Eastman.

The present contribution may be regarded as a continuation and enlargement of two previous articles on the Dinichthyids,[1] one of which discussed the relationships of certain detached and little known plates, and the other endeavored to trace the ancestry of the group. Some of the plates mentioned in the first paper are now illustrated and more fully described, together with others which afford additional evidence regarding the osteology of *Dinichthys;* and the views set forth in the second paper are now considered more in detail. In addition, descriptions are offered of several new species, and restorations are given of the dorsal and ventral aspects of *Dinichthys.*

Unless otherwise stated, the material upon which all of the following descriptions are based is preserved in the Museum of Comparative Zoölogy at Cambridge, Mass. To Mr. Alexander Agassiz, Director of the Museum, the most cordial and grateful thanks of the writer are due for the opportunity to study the collection, and to publish the results herein set forth.

Dorsal Plates. — It is proposed to consider first the system of plates covering the dorsal surface of the body in *Dinichthys.* These plates are shown in their natural arrangement, as known to exist in *D. intermedius* and *D. terrelli*, in Plate 1, Fig. 1; their correspondence with homologous elements in *Coccosteus* and related genera will be obvious from an inspection of the diagrams. The restoration here given may seem to call for a word of explanation, since it differs in certain respects from the familiar ones of Newberry and others.[2] The cranial osteology is based upon one of the most perfect heads of *Dinichthys intermedius* ever discovered, now the property of the Cambridge Museum. A full description of the same specimen has already been published by E. W. Claypole.[1] Inasmuch as this cranium lacks the marginal and suborbital plates, these have been supplied in the diagram from Newberry's restoration. The fact that they are shown more in projection than perspective imparts a wider and more flattened appearance to the cranium than is strictly natural; the dorso-laterals are likewise drawn as if flattened out, instead of conforming to the curvature of the body. The outline of the dorso-median has been reduced to scale from a photograph of an exceptionally perfect plate obtained from Dr. William Clark by the British Museum; its exact position as regards the dorso-laterals has been ascertained from specimens in the Museum of Comparative Zoölogy. Hence the restoration can be considered as such only in the sense that the parts are now brought together in their completeness and proper relationships, and are shown on the same scale.

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[1] Amer. Journ. Science, [4], Vol. II. pp. 46–50, July, 1896. Proc. Amer. Assoc. Adv. Science, Buffalo Meeting, August, 1896 (Abstract in Amer. Geol., Vol. XVIII. pp. 222, 223).

[2] Newberry, J. S., Palæozoic Fishes of North America (Monograph U. S. Geol. Survey, Vol. XVI. Plate LII. Fig. 2), 1889. Dean, B., Fishes, Living and Fossil, 1895, p. 134, Fig. 134.

The earlier restorations already referred to are subject to the following criticisms. First, the anterior portion of the dorso-median is produced in imagination so as to cover the exposed space behind the occipital region; secondly, the conditions of overlap and underlap are represented on only one side of the antero-dorso-lateral, instead of on three sides; thirdly, the postero-dorso-lateral is not shown at all.

Hitherto the postero-dorso-lateral has never been found in direct association with other plates, and its position has accordingly remained in doubt. It has long been known under Newberry's designation of "post-clavicular," and is a plate of not uncommon occurrence in the detached condition. Its triangular form, the markings impressed upon it by overlying plates, and the course of the sensory canal system across it, appeared to the writer[2] sufficient evidence for assigning the plate theoretically to the position indicated in the diagram; and it is therefore interesting to record the discovery of a specimen which establishes the entire correctness of this inference. The new specimen represents the right antero- and postero-dorso-lateral plates of *D. terrelli*, firmly articulated together, as shown in Plate 2, Fig. 1. It is from the Cleveland Shale, and was found in the vicinity of Lindale, Ohio, by Mr. Prentis Clark. The inner surface of the plates is alone visible, the external side being embedded in the matrix. The mode of articulation between the two plates is by pegs and sockets, the position of which is fairly constant among the specimens that have been observed. The largest and most perfect plate that the writer has seen is preserved in the Museum of Comparative Zoölogy, and measures 65 cm. in length (Catalogue No. 1325). The corresponding element in *D. intermedius* is hardly to be distinguished except for its smaller size. An excellent example of the latter species belonging to the School of Mines Cabinet of Columbia University shows the postero-dorso-laterals of either side of the body commingled with other plates pertaining to the same individual; it is valuable for furnishing comparative measurements of the different bones, and deserves further study.

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[1] Claypole, E. W., The Head of Dinichthys (Amer. Geol., Vol. X. p. 199), October, 1892.

[2] Amer. Journ. Science, [4], Vol. II. p. 48, July, 1896.

The orientation of the plate in question may be readily determined, either by an inspection of the overlapped area, or by noting the course of the sensory canals. These arise at the anterior border, where they meet the single straight furrow that traverses the antero-dorsal-lateral; and from this point they sweep inwardly, sometimes as a single and sometimes as a double channel, as far as about the middle of the exposed portion of the plate, where they cease. In this respect the genus differs from *Coccosteus*, which has the canals continued on to, and in some cases entirely across, the dorso-median. The insunken area formed by the overlap of the latter plate stands in marked contrast to the irregular depressions produced by the overlap of the antero-dorso-lateral. The graceful curve forming the postero-lateral boundary of the dorso-median is projected upon the underlying plate, and shallow depressions are left where the transverse ridge on the under surface of the dorso-median rested on the subjacent plate. This ridge, it should be noted, occupies the same relative position as its homologue in *Coccosteus.*

The upper boundary of the lateral plates is indicated by a deeply insunken area on the antero-dorso-lateral, and a slight indentation on the free margin of the postero-dorso-lateral. Below, these as yet undiscovered plates must have been connected with the ventral armoring, either directly, or more probably through the intervention of the "claviculars." The curvature of the ascending arm of the latter furnishes us at the same time with the curvature of the missing laterals, and we can also form an approximate estimate of their height and length. It is to be hoped that the laterals may yet be identified as such, when the entire dermal covering of *Dinichthys* can be compared plate for plate with its European congeners.

Ventral Plates. — Grave difficulties have been encountered in the attempt to reconstruct the ventral armor of *Dinichthys,* owing to the detached condition in which the plates have invariably been found. It is perhaps but natural that the views which were originally entertained regarding the structure of the plastron should have received important modifications in consequence of later discoveries. Thus, Newberry's supposed posterior ventrals were afterwards identified as the suborbitals, and his so called "jugulars" have since been demonstrated by Wright[1] to be in reality the posterior ventrals.

The restorations of Wright and Dean[2] (the latter being somewhat modified after Wright's figures) leave the median plate or plates unaccounted for, and it remained for Dean in a subsequent publication[3] to reconstruct the ventral covering afresh, with the addition of a single element along the median line. But as pointed out by the present writer in a review of Dean's article,[4] the evidence is not entirely conclusive that a distinct antero-median ventral was not present in advance of the posterior element and overlying it, although now obscured on the specimen by weathering. The writer has since had an opportunity for examining the original, which is referred by Dr. Dean with some hesitation to *Dinichthys gouldi*. Although it is badly fractured precisely at the spot where we should expect a suture to exist, and therefore incapable of affording positive proof on this point, nevertheless the fact that the two plates we know were at least potentially present should have retained their normal position with respect to each other, while the adjacent plates have become displaced, points strongly toward a union of some kind between them.

For an undoubted example of fusion of the mid-ventrals we must turn to the specimen of *Dinichthys terrelli* figured by Newberry on Chart VI. (Figure A), accompanying the second volume of the Ohio Geological Survey Report. The original is still preserved in the School of Mines Cabinet, and has been recently refigured by Dr. Dean.[5] The resemblance of the anterior and posterior portions to plates presently to be described, and occurring as distinct elements, is sufficiently obvious. In this specimen, and the statement doubtless applies to all adult individuals of the same species, fusion exists between the mid-ventrals; in *D. gouldi* fusion probably likewise exists. These two instances are sufficient, in Dr. Dean's estimation, to compel us "to accept the thesis that the median ventral plates of *Dinichthys* must be separate or fused in *all* members of the genus."

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[1] Wright, A. A., The Ventral Armor of Dinichthys (Amer. Geol., Vol. XIV. pp. 313–320), 1894. Report Ohio Geol. Survey, Vol. VII. pp. 620–626, 1893.

[2] Dean, B., Fishes, Living and Fossil, 1895, Fig. 135, p. 134.

[3] Dean, B., The Ventral Armoring of Dinichthys, etc. (Trans. N. Y. Acad. Sci., Vol. XV. pp. 157–163, May, 1896).

[4] Amer. Geol., Vol. XVIII. pp. 316, 317, 1896.

[5] Dean, B., Trans. N. Y. Acad. Sci., Vol. XVI. Plate III., 1897.

Under ordinary circumstances, such an interpretation would appear most logical, since we should expect, *a priori*, marked differences in the mode of union of the mid-ventrals to be indicative of different genera. We might reasonably infer that these differences were accompanied by variations in the dentition and other parts of the body, although this is a point which could only be determined empirically. Should it be ascertained, however, that forms existed having a like dentition, a like configuration and arrangement of plates as in *Dinichthys*, yet differing among themselves as respects the mode in which the median ventrals were united, there would be difficulty in estimating the value of this latter character. Ought it to be regarded as a valid generic distinction, or, other things being equal, merely as an adaptive variation affecting different species indiscriminately? From present indications it would appear highly probable that diverse conditions existed in the ventral plates of forms which agree in their remaining characters, so far as known, with *Dinichthys*. It must be noted, also, that amongst the species of this genus the paired ventral plates are exceedingly variable in their characters, more so in fact than any other plates of the body. Not only do they vary in form, relative proportions, and mode of union among different species, but there are considerable differences to be observed within one and the same species; one class of variations within specific limits will be referred to later under the head of ventro-lateral plates.

To sum up these difficulties briefly, we must admit on the one hand that theoretical considerations are opposed to the view that species of one and the same genus should differ widely as respects the number and arrangement of the median ventrals; but on the other hand, evidence is wanting to show that the forms they represent differed in any respects further than this from *Dinichthys*. And until positive evidence is forthcoming, such as finding the plates naturally associated with the dentition, it is impracticable to employ characters of the ventral plates as a test of generic rank. In our opinion, both prudence and convenience dictate that plates which resemble the known elements of *Dinichthys*, when found in the detached condition, are to be referred to that genus until criteria are at hand for determining them otherwise. Accordingly, certain isolated plates, whose description follows, will be referred to *Dinichthys* by virtue of their obvious affinities with that genus. And it will be assumed, provisionally at least, that in this genus the median ventrals may exist in three different conditions of union; they may simply overlap, as in *Coccosteus;* they may be fused into a single elongated piece; or they may be interlocked with one another. Examples of these three modes of union will now be considered.[1]

Interlocking Median Ventrals. — Two instances have been recorded where the median ventral plates of *Dinichthys* are articulated with one another; the first was made known by E. W. Claypole in 1893,[2] the second by the present writer in 1896.[3] In both cases the plates occurred in the detached condition, and were referred provisionally to the genus *Titanichthys.* Further investigation has since shown this to have been an erroneous determination, and the only genus that they can be certainly referred to in the present state of our knowledge is *Dinichthys.* The original of Professor Claypole's figure is preserved in the Museum of the Ohio State University at Columbus. It is a very large and heavy postero-ventro-median, and with it were associated the greater part of the postero-ventro-laterals. The proportions indicate a considerably larger species than either *D. terrelli* or *D. hertzeri,* and accordingly the name *D. ingens*[4] has been suggested for it by A. A. Wright. As a detailed description of these remains is in course of preparation by Professor Wright, it is sufficient for our purpose merely to cite this as an illustration of a particular mode of union between the median ventrals.

The other example of articulation or dovetailing is furnished by a specimen in the Museum of Comparative Zoölogy, now figured for the first time (Plate 2, Fig. 2). It is broadly lozenge-shaped, and its diagonals measure 20 by 31 cm. The resemblance of this plate to the posterior part of the single element in *D. terrelli,* already referred to, as figured by Newberry and Dean, is obvious. Its size, thickness, and markings impressed upon it by the paired ventrals, are also in substantial agreement. In these particulars it is seen to be closely allied to *D. terrelli;* but on the other hand the articulation with the antero-ventro-median is precisely the same as in *D. ingens.* The plate in question was collected by Mr. Terrell, in the Cleveland Shale of Lorain County, Ohio; but whether associated or not with other remains cannot now be ascertained. Theoretical considerations are certainly opposed to the idea that this plate pertained to either *D. terrelli* or *D. ingens;* and we are compelled to regard it as indicating an as yet unknown Dinichthyid species.

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[1] See abstract of a preliminary paper by A. A. Wright, entitled, "New Evidence upon the Structure of Dinichthys" (5th Ann. Rep. Ohio State Acad. Sci., 1897, pp. 59, 60).

[2] Report Geol. Survey of Ohio, Vol. VII. p. 611, Plate XL. Fig. 1.

[3] Amer. Journ. Science, [4], Vol. II. p. 47.

[4] Should an identity be established between these plates and the mandible described by Claypole as *D. kepleri,* the latter name is entitled to priority.

Fused Median Ventrals. — Under this head must be placed the two examples already referred to, that have been described by Newberry[1] and Dean.[2] The originals are preserved in the School of Mines Cabinet at Columbia University, and have been determined as *D. terrelli* and *D.* (?) *gouldi.* Whether fusion took place as a strictly adaptive character in forms having a thin plastron, whether it occurred only in adult individuals, or whether it characterized all the individuals belonging to particular species, are questions for future discoveries to determine. That fusion did not exist in all species of *Dinichthys* appears, however, extremely probable.

Overlapping Median Ventrals. — Species which have the postero-ventro-median overlapped by the anterior element represent the normal or primitive condition, as exemplified by the genus *Coccosteus.* Three specimens of the detached antero-ventro-median and two of the postero-ventro-median are preserved in the Cambridge collection, whose relations to contiguous plates were plainly those of overlap and underlap. The bone shown in Plate 2, Figs. 5, 6, exhibits such a striking resemblance to its homologue in *D. terrelli*, that there can be no doubt as to its identity. It is evident that the plate under discussion is entire, since its margins taper gradually to a thin edge, and show no signs of having been broken away from a lower portion. Hence, the only important difference that is to be observed between this specimen and *D. terrelli* relates to the mode of union with the posterior element; in the present case it overlaps, in *D. terrelli* it is fused with the hinder piece. As we know of no other species to which it can be referred, we must include it, provisionally at least, under the last named species.

The special characters of this plate have been described elsewhere, although at that time the specimen was supposed to belong to *Titanichthys.* It may be remarked in passing that the semicircular flange forming the anterior margin (seen best on the ventral aspect) is continuous with similar compressed borders on the antero-ventro-laterals. None of these margins reveal any trace of plates overlapping them in front; so that an interlateral element, such as is present in *Coccosteus*, cannot be said to exist. We are therefore limited to assigning a strictly lateral (external) position for the so called "claviculars" or coracoids.

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[1] Report Geol. Survey of Ohio, Vol. II. Part. II. (Palæontology), pp. 10, 31, and Chart VI. Fig. A.

[2] Trans. N. Y. Acad. Science, Vol. XV. pp. 157–163, 1896; Ibid., Vol. XVI. pp. 57–60, 1897.

A second specimen of the ventro-median preserved in the Cambridge collection (Catalogue No. 1299) shows the longitudinal ridge on the visceral surface more strongly developed than the first, and is both thicker and wider towards its posterior extremity.

There is yet a third specimen, which is smaller and of somewhat different configuration from the preceding; this is shown in Plate **3**, Fig. 1. The visceral surface is embedded in the matrix, so that its character cannot be made out. In form it is somewhat suggestive of the parasphenoid bone of *Ctenodus*, but its structure as seen under the lens proves it to be Dinichthyid. The plate was obtained by Dr. Clark in the Cleveland Shale, near Lindale, Ohio. Owing to its smaller size, it may be referred with some reservation to *D. intermedius*.

From the same locality as the preceding, Dr. Clark has also obtained two unique plates, one of which is preserved in counterpart, and is shown in Plate **5**, Fig. 1. Lanceolate in outline, and perfectly symmetrical, it presents a very graceful appearance; its length is 29 cm., and its maximum width 12.5 cm. Only the visceral aspect is exposed, and this is marked by two slightly oblique ridges, such as occur also in the corresponding position of *D. terrelli*. The plate is abruptly truncated in front, and bears indications of overlap by the antero-ventro-median. We shall find that additional light is thrown upon these relationships when we consider the plastron immediately to be described. The specimen is somewhat thinner than other ventral plates that have been noticed thus far, and it differs also in form. For the present, it must be regarded as representing an unknown Dinichthyid.

Overlapping Median Ventrals preserved in Situ.

So far, but two instances have been reported where the ventral plates were retained in their natural relations with respect to one another. The less perfect of these was described very briefly by von Koenen,[1] by whom it is doubtfully referred to *D. minor*. Only the left half of the plastron is preserved in this case; its entire length is assumed to have been about 16 cm., and its width 6 or 7 cm. The condition of the specimen is too imperfect to admit of a precise determination of the several elements, as the author has informed us by letter.

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[1] Koenen, A. von, Ueber einige Fischreste, etc. (Abhandl. Gesellsch. Wissen. Göttingen, Vol. XL. p. 18), 1895.

The only other instance recorded where the plastron has been preserved *in situ*, is that made known by the writer at the Buffalo Meeting of the American Association for the Advancement of Science. For the discovery of this interesting fossil, science is indebted to Mr. F. K. Mixer, Curator of the Buffalo Society of Natural Sciences, who found the slab in place at the bottom of a small stream bed near Sturgeon Point, on the lake shore, twenty miles west of Buffalo, N. Y. The horizon at this point is the black Portage Shale, which has already yielded a considerable number of fish remains.[1] The plates were correctly determined by Mr. Mixer to be of Dinichthyid nature, and were so labelled by him and placed on exhibition in the Museum of the Buffalo Society. To this enthusiastic collector the writer is greatly indebted for the privilege of studying the specimen, and of presenting the following description of it.

Although the fossil has suffered considerably from aqueous and atmospheric erosion, the salient features have been so far preserved as to furnish points of control sufficient for reconstructing almost the entire topography. The slight extent to which the diagram given in Plate 1 has been reconstructed may be seen from a comparison with a photograph of the actual fossil, reproduced in Plate 4. In most cases the sutural indications are so distinct, and continuous over such an area, that we have only to produce them in the same general direction across breaks in the surface until they meet, in order to complete the small portions that are interrupted. Thus, among the prominent landmarks that are left may be mentioned the terminal angles of the antero-ventro-laterals, which overlie the postero-ventro-laterals in their natural position. Half way between these points gives us the median line of the body; and as all the plates are arranged symmetrically with reference to it, it is clear that the fossil has been in no wise distorted. A knowledge of this fact permits us to supply the contours of one side from information derived from the other, and fortunately the two sides supplement each other to a remarkable degree. The only boundary lines that are not tolerably distinct are the forward portions of the antero-ventro-laterals. We will consider the relations of the different plates in order.

Ventro-Median Plates. — The first question that arises concerning the median ventrals is whether they are represented by one element or by two? And if two, what is their mode of union? We have no hesitation in answering that two median plates are present, and that the anterior overlaps the posterior, as in *Coccosteus*. The evidence appears perfectly decisive, and is of twofold nature; it depends upon a prominent surface elevation over the very region where we should expect the boundary between two median ventrals to be, and upon the fact that two centres of ossification are discernible.

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[1] Mixer, F. K., Amer. Geol., Vol. XVIII. p. 223, October, 1896. Williams, H. U., Bull. Buffalo Soc. Nat. Sci., Vol. V. pp. 81–84, 1886.

The surface elevation referred to is palpably of the same nature as those prominences which are formed by the hinder extremities of the antero-ventro-laterals where they are superimposed upon the posterior pair of ventro-laterals. All of these elevations are more or less eroded in the specimen, but the one under consideration is scarcely more so than the others. If it were a purely fortuitous bulge of the surface, we should expect similar ones to occur elsewhere, whereas the prevailing aspect of the plates is flat and smooth. But inasmuch as the only remaining elevations are found at those places where we know for certain that boundaries occur, and as this occurs at the only place in the median line where we should expect to find a boundary, we are compelled to look upon this as a significant, not an accidental feature. Moreover, the shape of the elevation corresponds with the tapering extremity of the antero-ventro-median, superimposed upon the posterior element; and the outline of the latter is seen to be perfectly normal as compared with homologous plates, when we cut it off at this point. In fact, it is noteworthy that the shape of the postero-ventro-median bears a marked similarity to the bone last described (*supra*, p. 26), and shown in Plate 5, Fig. 1.

But still more pertinent evidence as to the existence of two median ventrals is furnished by the structure of the plates themselves. It is apparent at a glance that in the postero-ventro-median ossification proceeded from a single centre, which was nearly coincident with the centre of the plate itself. On holding the slab so as to reflect light at a proper angle, the course of vascular (Haversian) canals can be seen very distinctly, especially at the right anterior boundary; and all of these radiate toward the centre of the plate. Vascular canals are likewise apparent on the antero-ventro-laterals, but are only faintly perceptible on the antero-ventro-median. If the latter plate were articulated or fused with the posterior element, as in *D. terrelli*, it would be difficult to account for the significant elevation already referred to; and considering the relative thinness of the plates, such a mode of union could hardly have proved advantageous. It is more natural to suppose that the connection among all plates of the ventral armoring was one of simple overlap, as in *Coccosteus* and other forms.

Ventro-Lateral Plates. — The inner margins of the antero-ventro-laterals are traceable with certainty throughout the greater portion of their length, but with a lesser degree of probability for the remaining (anterior) portion, where they are not only much abraded, but in part covered over by extraneous fragments, as will be noted presently. The boundaries of these plates are more sinuous than in any other known species, and their proportions with respect to the posterior pair are also different. But, as already remarked, the ventrals exhibit a greater range of variation, even within specific limits, than all the other plates of the body.

One class of variations that deserves notice here is the relative length of the two sets of ventro-laterals. Sometimes the anterior pair is the longer, and again, apparently within the limits of the same species, the posterior pair exceeds them in length.

Possibly these differences may have been correlated with sex, a greater portion of the abdomen having been protected in the one case than in the other;[1] but however this may be, we are obliged to recognize the existence of these two patterns or varieties of the plastron. The present specimen, therefore, belongs to that type of plastron which has the anterior ventro-laterals longer than the posterior.

The external margin of the postero-ventro-laterals appears to have been evenly rounded. Unfortunately, the central portion of the plates has been eroded away, so that the contour of the inner margins can only be postulated. It is probable, however, owing to the tenuity of these plates, that the condition of their union was one of simple overlap; hence Dean's figures of *D. gouldi* (?) have been followed in restoring their inner boundaries. Of the anterior borders of these plates, no trace whatever remains. There may be some significance attached to the fact that the antero-ventro-laterals are symmetrically worn away, their present eroded margins forming a regular curve from the ventro-median outward. Whether this symmetrical wearing away was in any respect influenced by the anterior margins of the hinder pair of plates may perhaps be questioned; but at all events we must conclude that the former anterior boundary of these plates was not far from, and was probably parallel with, the interrupted edges of the antero-ventro-laterals. That the plates in question were separated for a considerable distance posteriorly, is witnessed by an impression of the visceral surface of the ventro-median, which is preserved as far as its posterior apex on the slab.

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[1] Amer. Geol., Vol. XVIII. p. 317.

We have now to determine what species of *Dinichthys* is represented by the ventral armor just described. In the absence of the dentition, we must either associate the remains theoretically with mandibles of corresponding size that occur in the same horizon, or must regard the plastron as belonging to a new species. Fortunately, the proportions between the different body plates are well known in *D. terrelli* and *D. intermedius*, and from them we can readily compute the length of mandible and size of dorsal shield to which the present specimen would correspond. Thus, the ratio between the length of mandible and length of the antero-ventro-laterals in *D. terrelli*[1] is 1.14, and, assuming that about the same proportion held true for the species now under discussion, we should attribute it with a mandible 24 or 25 cm. long. Now, from the Genesee Shales near Bristol Center, New York, J. M. Clarke has described under the title of *D. newberryi* a mandible measuring 28⅓ cm. in length.[2] In the same horizon are also found detached dorsal shields which are considered by this writer as belonging to *D. newberryi*, although their dimensions correspond almost precisely with those of *D. minor*. In fact, Dr. Clarke's tables (pp. 22, 23) show that, while the mandibles of *D. newberryi* are about one half as large as in *D. hertzeri* and *D. terrelli*, the dorsal shields are less than one fifth the size of those in either species. Such a marked discrepancy of ratio appears incredible in the light of comparison with other species; and the measurements of the plastron now under discussion militate with the assumption that they, the mandibles of *D. newberryi*, and the dorsal shields from the same horizon as the last, all belonged to a single species. The correspondence of parts is such as to permit of a theoretical association of the plastron with the mandibles of *D. newberryi*, but not with the dorsal shields that are referred by Dr. Clarke to this species; these latter being more properly assignable to *D. minor*, or a species of equal size with *D. minor*.

It must be borne in mind, however, that these conclusions depend entirely upon empirical formulas; they are therefore more or less tentative and provisional. It may be presumed from the general nature of things, and in the absence of any contrary evidence, that the proportions existing between parts of the derm skeleton were fairly constant within the limits of one and the same genus. But the correspondence of parts as known in *Dinichthys* does not hold true by any means for other genera (*Trachosteus*, *Mylostoma*, etc.) belonging to the same family; and this fact admonishes us not to press hypothetical correlations too far, even within specific limits. Caution is enjoined in this particular case by yet another consideration. From the same locality and formation, Mr. Mixer has obtained a pair of mandibles associated with fragmentary Dinichthyid plates. The condition of these remains does not warrant a precise specific determination, but their affinities are probably with *D. minor*. The length of each ramus is about 17 cm., and the maximum height 5 cm. Either, therefore, these remains and the plastron represent together but a single species (*D.* ? *minor*), or we have evidence of two medium-sized species (*D.* ? *minor* and *D.* ? *newberryi*) in the Portage Shale.

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[1] Wright, A. A., Report Geol. Surv. Ohio, Vol. VII. p. 626.

[2] Clarke, J. M., Bull. U. S. Geol. Survey, No. 16, p. 17, 1885.

Under these circumstances it is apparent that a positive identification of the species is impossible. For the sake of convenience, we might follow Dr. Clarke's example, and refer all the detached plates occurring in the Genesee Shales to *D. newberryi*, and all those from Portage Shale to *D. minor*. But there is no reason for supposing that each of these horizons contains but a solitary species; the indications point rather to the presence of more than one species in both horizons. And there is no reason why the doctrine of correlation of parts should not be applied to all the species of *Dinichthys* until experience has shown it to be invalid for some of them. Provisionally, therefore, we are in favor of referring the Portage plastron to the species with which it most closely agrees in measurement and geological horizon, that is to say, with *D. newberryi*. On the other hand, the Portage mandibles that have just been mentioned, and the detached dorso-median plates from the Genesee, may be referred provisionally to *D. minor*.

Comparative measurements of certain derm-plates for several species of *Dinichthys* are exhibited by the table on the following page.

Besides the plastron just described, there are several other interesting structures preserved on the same slab. In advance of the plastron are a number of badly weathered fragments, which evidently represent the dorsal plates of the body. The forward portions of both antero-ventro-laterals are covered over, and their proper boundaries obscured, by some of these fragments; but none of them are identifiable with certainty unless it be the antero-lateral tip of the dorso-median, which rests upon the angle of the right antero-ventro-lateral. This concealment of the underlying plates along their margins is unfortunate, since the restored anterior boundary has not such a clear basis of fact as one could wish

Comparative Measurements of Dinichthys Species.

No.	Species.	I. Length of Mandible.	II. Length of DM.	III. Length of DM without carinal process.	IV. Width of DM.	V. Length of A. V. L.	VI. Length of P. V. L.	VII. Length of Plastron.	VIII. Ratio between Columns II. and VII.
1	*D. ingens* . . .	. .	. .	. .	. .	. .	76 +		
2	" *hertzeri* . . .	59.0	67.5	. .	53.0				
3	" *terrelli* . . .	56.25	65.0	36.0	57.5				
4	" " . . .	36.83	48.26	33.02	43.18	40.91	40.64	69.85	1.45
5	" " . . .	. . .	. .	. .	. .	48.26	55.88	90.17	1.87
6	" *newberryi* . .	28.33							
7	Portage plastron	. . .	. .	. .	. .	20.0	17.0	30 +	
8	*D. gouldi* . . .	17–20	. .	. .	. .	. .	12.6	8 +	
9	" *intermedius* .	22.86	41.91	29.21	26.67	17.15	22.86	35.56	0.85
10	" *minor* . . .	10 +	20.32	12.2	13.15	. .	. .	. .	1.59
11	Detached DM of Genesee Shale	. . .	. .	12.5	13.75				

for. At the same time it must be remembered that the front margin of the plastron in all species of *Dinichthys* conforms to a peculiar and well marked type.

To the right of the left antero-ventro-lateral is a small cleaver-shaped plate (7.5 cm. long by 3 cm. wide), the like of which is unknown among the derm plates of Coccosteids. It certainly does not belong to the dental apparatus, and is excluded from the orbital region on account of its size. There can be no doubt that the plate is entire, or nearly so; but we must confess ignorance as to its position on the body. Just behind the unidentified plate is to be seen a small portion of the vertebral axis, very imperfectly preserved, together with supports for the dorsal fin. The form of the neural arches is shown with some distinctness, as well as their articulation with the proximal row of basal cartilages. The outer tips of the distal row of basals appear to have been bluntly terminated, or even swollen.

DESCRIPTIONS OF NEW SPECIES.

Under this heading are included, besides species altogether new to science, certain others which are now demonstrated for the first time to belong to the genus *Dinichthys.* The subject may be properly introduced by a consideration of the latter forms first.

As is well known, a large number of genera and species of Arthrodires have been founded on detached fragments, which commonly yield but little insight into the structure of the fish as a whole. Sometimes our knowledge of these forms is increased by the discovery of more perfect specimens, or by finding parts in natural association with the dentition or with other parts. The dentition obviously yields the most trenchant characters that can be employed for the discrimination of species; but in *Dinichthys* scarcely less important characters are furnished by the dorso-median plate. Owing to the massiveness of this plate, it is not readily subject to fracture or distortion, and is perhaps of more frequent occurrence than any other plate in the body. Its configuration varies markedly amongst the different species of *Dinichthys*, but remains fairly uniform within the limits of one and the same species; hence its systematic importance is very great.

There is one feature about the dorso-median which appears to be peculiar to the Dinichthyids; or, to put it differently, the Dinichthyids are distinguished from remaining Coccosteids by the possession of a certain characteristic structure; and this is the large, excavated carinal process by which the dorsal shield is terminated posteriorly. (See Plate **2**, Figs. 3, 4; Plate **3**, Figs. 2, 3.) All of the *Coccosteidæ*, so far as known, have a median longitudinal keel or ridge on the inferior surface of the dorso-median; but it is developed to a different degree, and is terminated in a different manner, amongst the several genera. In *Coccosteus* it ends posteriorly in a simple blunt spine; in *Homosteus* the ridge is stronger, and terminates in a knob at the posterior border of the shield; and in *Heterosteus* the keel is greatly developed, but is not produced behind the margin to any great extent, nor is it excavated superiorly. This series of Coccosteid genera leads up to the conditions that exist in the Dinichthyid group, where the inferior ridge is terminated posteriorly by a distinct process, such as is unknown in other members of the family. If we arrange the Dinichthyid forms in order of relative development of the carinal process, we shall have the following series: *Coccosteus* sp. Pander (hereinafter described as *D. livoni-*

cus); a form from the Eifel Devonian, described below as *D. pelmensis; Pelecyphorus* Trautschold; *Asterolepis bohemica* Barrande (hereinafter described as *D. bohemicus*); *Dinichthys;* and lastly, the genus *Titanichthys*, which is so closely allied to *Dinichthys* as to pass for a mutation or modification of the same. *Titanichthys* is, essentially, a huge *Dinichthys* with lighter bones and a degenerate dentition. It is presumable that when the osteology of *Brontichthys, Gorgonichthys, Mylostoma, Trachosteus*, and related genera, shall have become known as fully as in *Dinichthys*, their affinities with one another will be found to be much closer than with the more primitive Coccosteids. Newberry was inclined to regard these forms as constituting a distinct family, the *Dinichthyidæ;* but that would rather overreach the mark. We venture to adopt the middle course, and assign to the forms enumerated above the rank of a subfamily, known as the *Dinichthyinæ.*

As already remarked, we may regard the presence of a carinal process as sufficient ground for referring detached dorso-median plates to the *Dinichthyinæ*, instead of the *Coccosteidæ* in general. For precise generic determination, a knowledge of the dentition is of course necessary; but where we are in ignorance of the dentition, we may conveniently place all species founded upon such dorsal shields, for the time being at least, under the single genus *Dinichthys.* Precedent for this is already furnished by *D. precursor, D. ringuebergi, D. tuberculatus*, and the plates from the Genesee Shale referred to above as *D.* (?) *minor.* To this category may now be added the following new species: *D. livonicus, D. trautscholdi, D. pelmensis*, and *D. pustulosus.*

Dinichthys livonicus nomen nov.

1857. *Coccosteus* aus Livland, C. H. Pander, Ueber die Placodermen des devonischen Systems, p. 70, Plate B, Fig. 4.
1889. *Coccosteus*, H. Trautschold, Ueber Coccosteus megalopteryx, etc. (Zeitschr. deutsch. geol. Gesellsch., Vol. XLI. p. 38).
1896. *Dinichthys livonicus*, C. R. Eastman, Observations on the Dorsal Shields in the Dinichthyids (Amer. Geol., Vol. XVIII. p. 222).

The original of Pander's Plate B, Fig. 4, of his Placodermen des devonischen Systems, may be taken as the type of this species, and there may be presumably associated with it the specimen referred to by A. S. Woodward (Brit. Mus. Cat. No. P. 4731), in his Catalogue of Fossil Fishes, Vol. II. p. 293. Without doubt this represents one of the smallest and most primitive species of *Dinichthys*, yet its marked development of the carinal process in proportion to its size is sufficient reason for excluding it from *Coccosteus.* It apparently has much in common with the type of dorso-median described by Trautschold as *Pelecyphorus*, but may best be considered as representing a distinct species.

Formation and Locality. — Devonian; Livonia and Government of St. Petersburg.

Dinichthys trautscholdi nomen nov.

1889. *Coccosteus megalopteryx*, H. Trautschold, Ueber Coccosteus megalopteryx, etc. (Zeitschr. deutsch. geol. Gesellsch., Vol. XLI. pp. 38–45, Plate V. Figs. 1–6.)

1890. *Coccosteus megalopteryx*, O. Jaekel (Neues Jahrb., Vol. II. p. 145).

1890. *Pelecyphorus*, H. Trautschold (Zeitschr. deutsch. geol. Gesellsch., Vol. XLII. p. 576).

1891. *Pelecyphorus*, G. Gürich, Ueber Placodermen und andere Fischreste im Breslauer mineralogischen Museum (Zeitschr. deutsch. geol. Gesellsch., Vol. XLIII. p. 906).

1896. *Dinichthys trautscholdi*, C. R. Eastman, Observations on the Dorsal Shields in the Dinichthyids (Amer. Geol., Vol. XVIII. p. 222).

The type specimens represented in Plate V. Figs. 1–6 of Trautschold's paper on *Coccosteus megalopteryx* (*loc. cit.*, 1889), are now preserved in the Breslau Museum. They are from the Devonian of the River Ssjass, in Northwest Russia, and are apparently very closely related to the foregoing species. The principal differences consist in the larger size and less strongly arched condition of the dorso-median proper, and the different shape and position of the carinal process. The latter is more deeply excavated on its posterior face, stands nearly at right angles with the surface of the shield proper, and is given off from it slightly in advance of the hinder margin of the same. In this last respect we find a resemblance to the dorso-median described by Newberry as *D. precursor;* and, as in most American species, the process bears distinct traces on its inferior surface of the attachment of muscles (Trautschold, *loc. cit.*, Plate V. Fig. 6). On the other hand, *Coccosteus*-like affinities are shown by the tuberculated surface of the dorso-median, and by the presence upon it of sensory canals. These curve around toward one another posteriorly, but are not continued across the middle of the shield. The development of the inferior ridge and its terminal process is very pronounced. The dimensions of the largest process observed by Trautschold are stated to be 6.5 cm. in height by 3 cm. in width at the base, — proportions which are eminently Dinichthyid.

This species, which it seems proper to name in honor of its original describer, Professor Trautschold, was confused by this author with a Selachian ichthyodorulite which he mistook for a swimming appendage of *Coccosteus*. Later, when it was pointed out that *Coccosteus* could not properly include either of these forms, a new generic title was proposed for each, — *Megalopterix* for the ichthyodorulite (afterwards discovered to be identical with *Psammosteus*), and *Pelecyphorus* for the dorsal shields. Curiously enough, the species were left unnamed in both cases, except that provision was made for calling them both *Megalopterix securigera* in the event of their being proved to represent but a single species of one and the same genus. The generic title *Pelecyphorus* is preocupied.

Formation and Locality. — Devonian; River Ssjass, Government of St. Petersburg.

Dinichthys pelmensis sp. nov.

Plate 2, Fig. 4.

The type of this species is represented by a specimen in the Schultze Collection belonging to the Museum of Comparative Zoölogy (Cat. No. 1375). It is from the Middle Devonian of Pelm, in the Eifel.

The greater portion of the left side of the dorso-median is preserved entire, but on the right side there remains only an impression of the under surface of the bone. The carinal process is admirably preserved, and is of large size in proportion to the dorsal shield proper. It is deeply hollowed out posteriorly, and stands less nearly perpendicular to the surface of the shield than in the two preceding species. The height of the process is 1.2 cm., and its maximum breadth 0.5 cm. The shield proper is 5.0 cm. long, and rather less than 4.5 cm. broad anteriorly. It is slightly arched transversely, and appears to have been emarginate in front. The sensory canals are distinctly traceable as far as the bone is preserved. That on the left side is seen to begin at a point about half way between the antero-posterior extremities of the shield, whence it continues nearly parallel with the postero-lateral margin of the same, but stops short of the median line shortly in advance of the process. Only the bare termination of the canal belonging to the right side is preserved on the present specimen. The surface of the plate is covered with fine reticulating ridges, at the intersections of which traces of minute tubercles are discernible. The effect of weathering, however, has been to reduce these, so that to the unaided eye the surface appears to be finely granulated. The thickness of the plate does not exceed 2 mm. except in the vicinity of the median longitudinal ridge.

Formation and Locality. — Middle Devonian; Eifel District.

Dinichthys eifeliensis Kayser.

Plate 3, Fig. 3; Plate 5, Fig. 4.

1880. *Dinichthys eifeliensis*, E. Kayser, Zeitschr. deutsch. geol. Gesellsch., Vol. XXXII. p. 817.

1895. *Dinichthys eifeliensis*, A. von Koenen, Ueber Fischreste des norddeutschen und böhmischen Devons (Abhandl. Ges. Wissensch. Göttingen, Vol. XL. pp. 16–18, Plate IV. Figs. 4, 5; Plate V. Fig. 1).

The mandibles of this species are estimated by von Koenen to have measured upwards of 50 cm. in length, and as it is the only Dinichthyid previously known with certainty from this locality, we may safely refer to it the specimens figured in the accompanying plates. That shown in Plate **3,** Fig. 3, represents without doubt the carinal process of a large dorsal shield, such as could well have belonged to a species as large as *D. eifeliensis.* Two or three additional specimens of the process, and several detached plates that are referable to the same species, also form a part of the Schultze Collection. One of these, identifiable as the right antero-ventro-lateral, is shown in Plate **5,** Fig. 4.

Formation and Locality. — Middle Devonian; Gerolstein, Berndorf, and elsewhere in the Eifel District.

Dinichthys bohemicus (BARRANDE).

Plate 2, Fig. 3; Plate 5, Fig. 2.

1872. *Asterolepis bohemica,* J. Barrande, Système Silurien de la Bohême, Vol. I. Suppl., p. 637, Plate XXIX. Figs. 9–13.
1880. *Asterolepis bohemica,* A. von Koenen, Abhandl. Ges. Wissensch. Göttingen, Vol. XXX. p. 4.
1895. *Anomalichthys bohemicus,* A. von Koenen, Abhandl. Ges. Wissensch. Göttingen, Vol. XL. pp. 8, 21.

There can be no difficulty in recognizing the form commonly known as *Asterolepis bohemica* Barr., since fossil fishes are not numerous in the Devonian of Bohemia, and this one is distinguished by its peculiar ornamentation. The tubercles are rather closely set, conical, and their summits, instead of being smooth, are finely punctate. The plates are of relatively large size, and usually exhibit considerable convexity.

There are two specimens of the dorso-median preserved in the Schary Collection, now the property of the Museum of Comparative Zoölogy, besides the impression of a third plate supposed to be one of the ventro-laterals. They are all from the same horizon, and two are from the identical locality as Barrande's type specimens. As has already been pointed out by von Koenen (*loc. cit.*, 1895, p. 8), it is extremely improbable that the figures given by Barrande are of the dorso-median. Their lack of bilateral symmetry, and their relative thinness, compel us to locate them elsewhere, perhaps on the ventral surface.

Certain it is, however, that the specimens shown in the accompanying figures represent the median dorsal plate. Not only do they fulfil the requisite conditions of shape, symmetry, and thickness, but both of them present fractures on the posterior end, where the carinal process has been broken off, leaving a cross-section of the inferior longitudinal ridge. On the strength of this evidence we are obliged to assign the species to *Dinichthys.* One of the plates has the inferior ridge much more strongly developed than the other, and differs considerably in form. But the ornamentation is essentially the same, and we are content to refer them both to *D. bohemicus,* since the coinage of new specific titles to include uncharacteristic fragments is greatly to be deprecated. Barrande's *Coccosteus fritschi*, as von Koenen has already surmised, is probably founded on the dorso-median of *Aspidichthys*.

Formation and Locality. — Middle Devonian (Étage Gg^1); Bohemia.

Dinichthys tuberculatus Newb.

1888. *Dinichthys tuberculatus*, J. S. Newberry, On the Fossil Fishes of the Erie Shale of Ohio (Trans. N. Y. Acad. Sci., Vol. VII. p. 179).

1889. *Dinichthys tuberculatus*, J. S. Newberry, Palæozoic Fishes of North America (Monogr. U. S. Geol. Surv., Vol. XVI. pp. 98, 99, Pl. XXXII. Fig. 3).

1889. *Dinichthys pustulosus* (*errore*), M. Lohest, De la découverte d'espèces américaines de poissons fossiles dans le Dévonien supérieur de Belgique (Bull. Soc. Géol. Belge, Vol. XVI. p. lvii).

1892. *Dinichthys pustulosus* (*errore*), [E. D. Cope], American Devonian Fishes found in Belgium (Amer. Naturalist, Vol. XXVI. p. 1025).

It is proper to record this species in connection with the foregoing, not only in order to complete the list of European representatives of the genus, so far as they have been described, but also because this is the only species of *Dinichthys* which is known to be common to both continents. This form may be regarded as the connecting link between the Old World species and the New; not that all the American Dinichthyids were derived from this species, but that this is one of the bonds through which the ancestry of the Western fishes can be traced backward to its starting point in Northern Europe. This chain of forms leads us eastward from Manitoba, through Iowa, Wisconsin, and Ohio, to New York and Pennsylvania; from the last named State *D. tuberculatus* carries us across the Atlantic to Belgium; next we meet with *D. eifeliensis* and *D. pelmensis* in Germany, followed by one species in Bohemia; and finally we come up with *D. trautscholdi* and *D. livonicus* associated with the ancestral *Coccosteus* and other derivatives from the same stock in the Devonian of Northwest Russia.

Formation and Locality. — Chemung Group; Pennsylvania. Psammite de Condroz; Belgium.

It remains only to present a description of certain Dinichthyid remains from the Hydraulic Limestone beds of Milwaukee, Wisconsin, a locality from which none have hitherto been known.

Dinichthys pustulosus sp. nov.

Plate 3, Fig. 4.

The F. H. Day Collection, purchased by the Museum of Comparative Zoölogy in 1881, contains a number of fish remains from the Hydraulic Cement Quarries near Milwaukee, Wisconsin. Among them are two plates whose preservation is such as to warrant description, especially since up to the present time but two species (*Rhynchodus greenei* and *Heteracanthus politus*) have been noticed from this locality.

The first of these (Plate **3**, Fig. 4) is easily recognizable as the left antero-dorso-lateral of a new species of *Dinichthys*, and is chiefly remarkable for its finely tuberculated style of ornament. This plate is nearly twice the size of the corresponding element described by Newberry as *D. tuberculatus*, its articulating condyle is differently situated, and the tuberculation is entirely dissimilar. Of *D. tuberculatus*, Newberry[1] speaks as follows: "The tuberculation of the surface is relatively coarse, and the tubercles vary much in size and are irregularly scattered. Most of them seem to be hemispherical and plain, but others are more or less pitted, and a few are stellate." In the present species the tubercles are small and closely crowded, and are distinctly stellate at their bases.[2] It is somewhat surprising that there should be so few American species which present the characteristic surface ornamentation of the *Coccosteidæ*; the inference is that the tuberculated are more primitive than non-tuberculated forms.

A longitudinal fracture traverses the plate to the left of the sensory canal. It is interesting in that it displays very clearly the course of the vascular (Haversian) canals, which run essentially parallel with the surface of the plate. The canals are also well shown where the articulating condyle has broken off; and from their direction it would appear that the plate had grown by increments to the visceral surface only.

The second specimen in this collection that deserves notice is evidently the impression of one of the ventral plates, probably the left antero-ventro-lateral, the substance of the bone itself being entirely worn away. The surface ornament cannot be discovered from this specimen, but several fragments associated with it exhibit the same tuberculation as occurs on the antero-dorso-lateral just described. The only reason for disassociating the two specimens specifically is that they represent individuals of somewhat different size; but the disproportion does not appear of itself sufficient ground for separation. The supposed antero-ventro-lateral measures 23 cm. in length by 11 cm. in width at about the middle of the plate. How much of the anterior portion is wanting cannot be accurately determined. Another large specimen from the same locality is to be seen on exhibition in the United States National Museum, at Washington, D. C., bearing the catalogue number 14,821.

Fragments of various size, and indistinguishable from this species so far as one may judge from the ornamentation, have been collected by the writer in the State Quarry fish-bed, near North Liberty, Iowa.[3] Other remains have been found in the Cedar Valley Limestone of the same State by Professor Samuel Calvin. One of the largest of these, which belongs to the State University Museum, shows the posterior portion of the cranium above and below very satisfactorily.

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[1] Newberry, J. S., Palæozoic Fishes of North America (Monogr. U S. Geol. Surv., Vol. XVI. p. 99), 1889.

[2] The artist has represented these somewhat diagrammatically in Figure 4, with the result of imparting a rougher aspect to the plate than is natural, although it is plain that the original has suffered somewhat from abrasion.

[3] See notes "On the Occurrence of Fossil Fishes in the Devonian of Iowa," appended to Report on the Geology of Johnson County (pp. 108–116), by Samuel Calvin, State Geologist. 1897.

There is good reason for believing that this species also occurs in the Hamilton of New York State. Mr. F. K. Mixer, who has made a careful search for fish remains in the vicinity of Buffalo, has obtained certain fragments from the Encrinal Limestone near the mouth of Eighteen Mile Creek, which exhibit almost precisely the same style of ornamentation, and agree furthermore in size with *D. pustulosus.* One of these fragments is identifiable as the suborbital plate, and shows very distinctly the sensory canals. Another represents about one half of one of the ventro-lateral plates, is rabbeted upon the edges, and shows some variation in the size of its tubercles. Again we notice that tuberculation of the ventral plates bears witness to primitive conditions. The ventro-lateral measures 21 cm. in maximum width, and is traceable for about the same distance in a longitudinal direction, the remaining portion being broken away. It is to be hoped that further and better preserved material will be forthcoming from this horizon, since by reason of their greater antiquity and primitiveness Hamilton Dinichthyids are likely to prove even more interesting than those of Upper Devonian age. In the event of these plates being proved by future discoveries to belong to a species distinct from *D. pustulosus,* with which they are now provisionally associated, it is but fitting to reserve the name *D. mixeri* for the New York species, in honor of the gentlemen to whom we are indebted for our first knowledge of it.

The title of *D. pustulosus,* although misapplied by M. Lohest for *D. tuberculatus,* has never been defined, and we are accordingly at liberty to appropriate it for the present species.

Formation and Locality. — Hamilton Limestone; Wisconsin, Iowa, and New York (?).

In this connection a word may be said concerning another plate discovered by Mr. Mixer, near Sturgeon Point on the shore of Lake Erie. The fossil is embedded in a loose block derived apparently from the Portage Shale, exposures of which occur at this locality. It presents the inferior aspect of a small dorsomedian plate, which is worn away anteriorly in such fashion as to reveal an impression of the external surface. This is seen to be finely tuberculated, and a few tubercles are left on an impression of a small plate (antero-dorso-lateral ?) adjoining the first. The longitudinal carina and its terminal process are both indicated, although the latter is partly fractured. The plate is quite thin; and this fact, together with its small size, fine tuberculation, and other characters, renders it probable that it belonged to an immature individual. It may be referred with considerable certainty to *D. ringuebergi,* a species which until the present time has rested upon a solitary dorsal shield from the same locality. Mr. Mixer's specimen is about one fourth smaller than the type, however, and is of more slender construction. If properly regarded as a young individual, it is interesting as being one of the few that are known.

It is evident from the figures of the type specimen of *D. ringuebergi*[1] that the carinal process has been considerably eroded, and the diagram of the inferior surface is not wholly accurate. If the anterior margin is entire, as represented for this species, it covers the region back of the head almost as completely as in *Coccosteus*. The type specimen is preserved in the private collection of its first describer, Mr. E. N. S. Ringueberg, at Lockport, New York. All of the specimens discovered by Mr. Mixer that are mentioned in the present paper are preserved in the collection of the Buffalo Society of Natural Sciences.

Another very beautiful example of a young Dinichthyid is preserved in the Museum of Oberlin College, and through the courtesy of Professor A. A. Wright we have been enabled to reproduce a photograph of it, shown in Plate **5**, Fig. 3. It is only about 5 cm. long, and 4.5 cm. in maximum width; the external surface is non-tuberculated. Unfortunately the terminal process is missing, but the inferior carina is very distinct. It is also seen to be strongly emarginate in front.

The drawings for Plates **1** to **3** have been executed by Messrs. C. A. King and J. W. Folsom. Plates **4** and **5** are reproduced from photographs of the original specimens, taken by Dr. T. A. Jaggar, Jr., excepting Figure 3 of Plate **5**.

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[1] Amer. Journ. Science, [3], Vol. XXVII. p. 477, June, 1884.

LIST OF AMERICAN SPECIES OF DINICHTHYS.

1. *D. canadensis* Whiteaves,	Upper Devonian, Manitoba.
2. *D. clarki* Claypole,	Cleveland Shale, Ohio.
3. *D. corrugatus* Newberry,	Cleveland Shale, Ohio.
4. *D. curtus* Newberry,	Cleveland Shale, Ohio.
5. *D. gouldi* Newberry,	Cleveland Shale, Ohio.
6. *D. gracilis* Claypole,	Cleveland Shale, Ohio.
7. *D. hertzeri* Newberry,	Huron Shale, Ohio.
8. *D. ingens* Wright (MS.),	Cleveland Shale, Ohio.
9. *D. intermedius* Newberry,	Cleveland Shale, Ohio.
10. *D. kepleri* Claypole,	Cleveland Shale, Ohio.
11. *D. lincolni* Claypole,	Marcellus Shale, New York.
12. *D. minor* Newberry,	Cleveland Shale, Ohio.
13. *D. newberryi* Clarke,	Genesee and (?) Portage Shales, New York.
14. *D. precursor* Newberry,	Corniferous Limestone, Ohio.
15. *D. prentis-clarki* Claypole,	Cleveland Shale, Ohio.
16. *D. ringuebergi* Newberry,	Portage Shale, New York.
17. *D. terrelli* Newberry,	Cleveland Shale, Ohio.
18. *D. tuberculatus* Newberry,	Chemung Group, Pennsylvania.
19. *D. pustulosus* nobis,	Hamilton Limestone, Wisconsin, Iowa, and (?) New York.

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PLATE 1.

Fig. 1. *Dinichthys intermedius* Newb. × $\frac{1}{6}$. Projection of cranium and dorsal plates in their natural relations with respect to one another. *DM,* Dorso-median; *ADL,* Antero-dorso-lateral; *PDL,* Postero-dorso-lateral. Sensory canals indicated by double dotted lines, boundaries of plates by single lines. The posterior process depends at an angle of about 60° from the plane of the dorso-median.

Fig. 2. *Dinichthys* (?) *newberryi* Clarke. × $\frac{1}{3}$. Restoration of the Portage plastron shown in Plate **4**. *AVM,* Antero-ventro-median; *PVM,* Postero-ventro-median; *AVL,* Antero-ventro-lateral; *PVL,* postero-ventro-lateral. Radiating lines show approximately the course of vascular canals. Overlapped borders of plates indicated by dotted lines.

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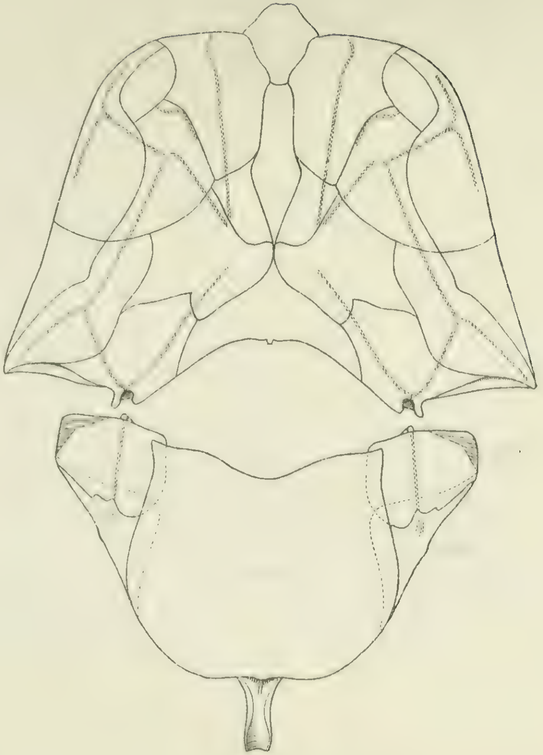

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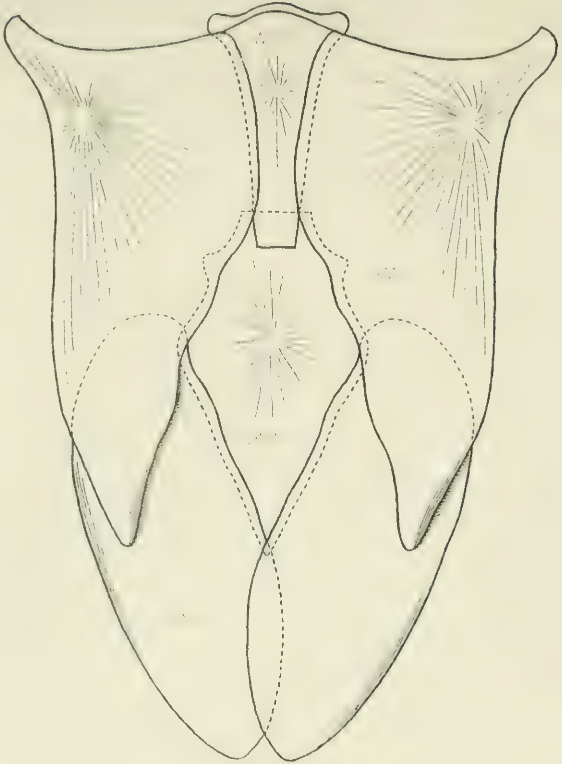

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PLATE 2.

Fig. 1. *Dinichthys terrelli* Newb. × $\frac{1}{4}$. Cleveland Shale; Lindale, Ohio. M. C. Z., Cat. No. 1379. Fragment showing internal surface of antero- and postero-dorso-lateral plates preserved in natural association with each other. Their union by pegs and sockets, the sinuous lateral boundary of the posterior plate, and the base of articulating condyle of the antero-dorso-lateral, are noteworthy features.

Fig. 2. Postero-ventro-median plate of an indetermined Dinichthyid species, from the Cleveland Shale of Lorain County, Ohio. × $\frac{1}{5}$ (approximately). M. C. Z., Cat. No. 1300. The external surface, shown here, bears impressions of overlapping plates, and is notched in front for reception of the antero-ventro-median.

Fig. 3. *Dinichthys bohemicus* (Barr.). × $\frac{2}{3}$. Middle Devonian (Étage Gg^1); Svagerka, Bohemia. M. C. Z., Cat. No. 1377. Tuberculated dorso-median plate. The posterior portion of the specimen, which was fractured obliquely downward, has been ground smooth and polished, so as to show the inferior carina in section.

Fig. 4. *Dinichthys pelmensis* sp. nov. × $\frac{1}{1}$. Middle Devonian; Pelm, Eifel District. M. C. Z., Cat. No. 1375. Dorso-median plate with perfectly preserved carinal process, and faint indications of sensory canals.

Fig. 5. *Dinichthys terrelli* Newb. × $\frac{1}{5}$. Cleveland Shale; Lorain County, Ohio. M. C. Z., Cat. No. 1301. Antero-ventro-median plate, seen from the external surface. Thickness at posterior tip less than 2 mm.; the plate has every indication of being entire, or very nearly so.

Fig. 6. Same specimen as shown in Fig. 5, viewed from the internal or visceral side. The thickened T-shaped ridge seen on this surface is very characteristic.

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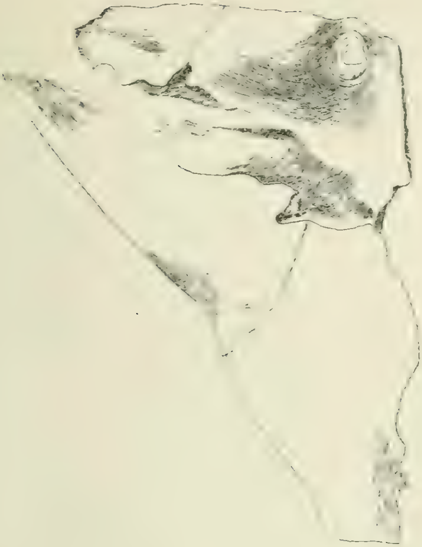

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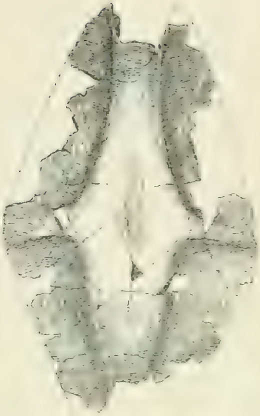

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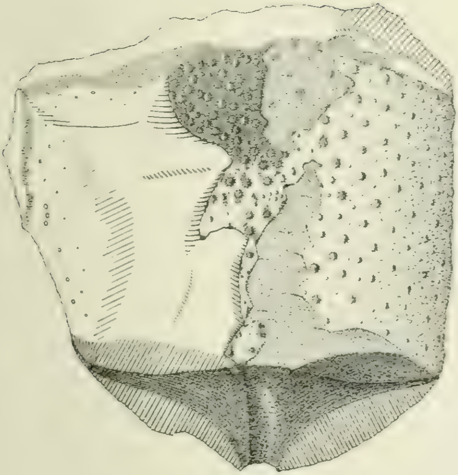

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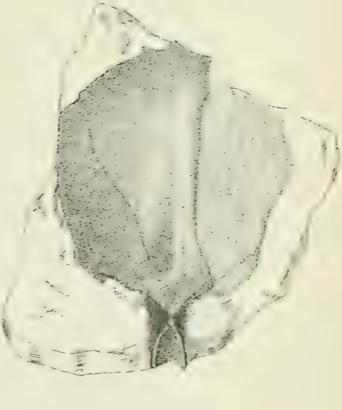

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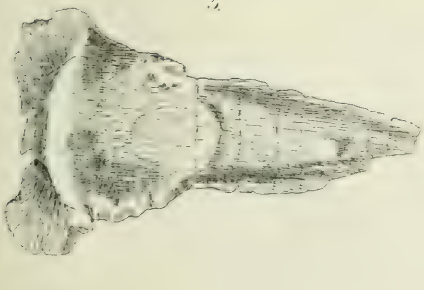

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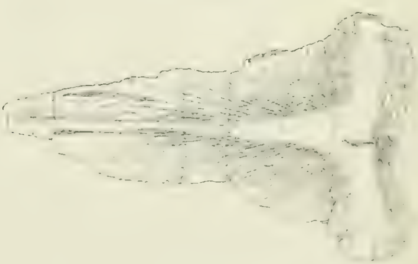

PLATE 3.

Fig. 1. *Dinichthys* (?) *intermedius* Newb. × $\frac{3}{4}$. Cleveland Shale; Lindale, Ohio. M. C. Z., Cat. No. 1380. External aspect of supposed antero-ventro-median plate.

Fig. 2. *Dinichthys terrelli* Newb. × $\frac{1}{3}$. Cleveland Shale; Lorain County, Ohio. M. C. Z., Cat. No. 1315. Posterior aspect of carinal process belonging to a large-sized dorso-median, viewed in a vertical position. The semicircular incision below, where it overrode the vertebral axis, its massive character, and depth of posterior cavity, are remarkable. It projects downward and backward at an angle of about 60° with the plane of the dorso-median, traced along the median line of the back.

Fig. 3. *Dinichthys eifeliensis* Kayser. × $\frac{1}{1}$. Middle Devonian; Berndorf, near Hillesheim, Eifel District. M. C. Z., Cat. No. 1374. Carinal process detached from dorso-median plate.

Fig. 4. *Dinichthys pustulosus* sp. nov. × $\frac{1}{1}$. Hamilton Limestone; Cement Quarries, Milwaukee, Wisconsin. M. C. Z., Cat. No. 1381. Slightly abraded antero-dorso-lateral plate, showing single sensory canal, and relatively fine tuberculation.

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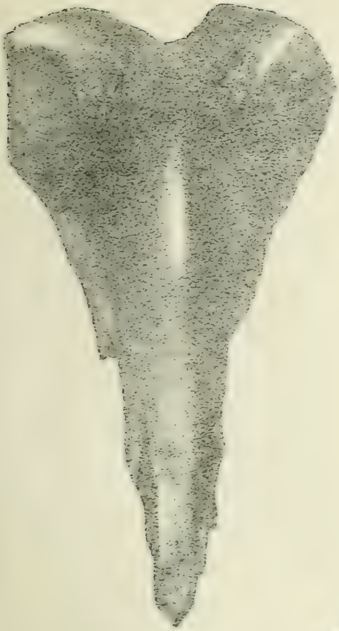

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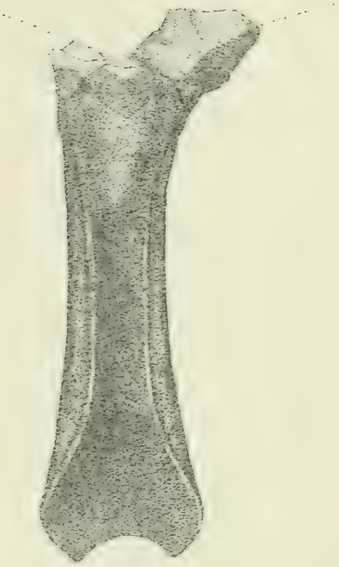

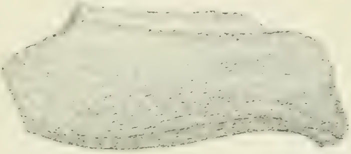

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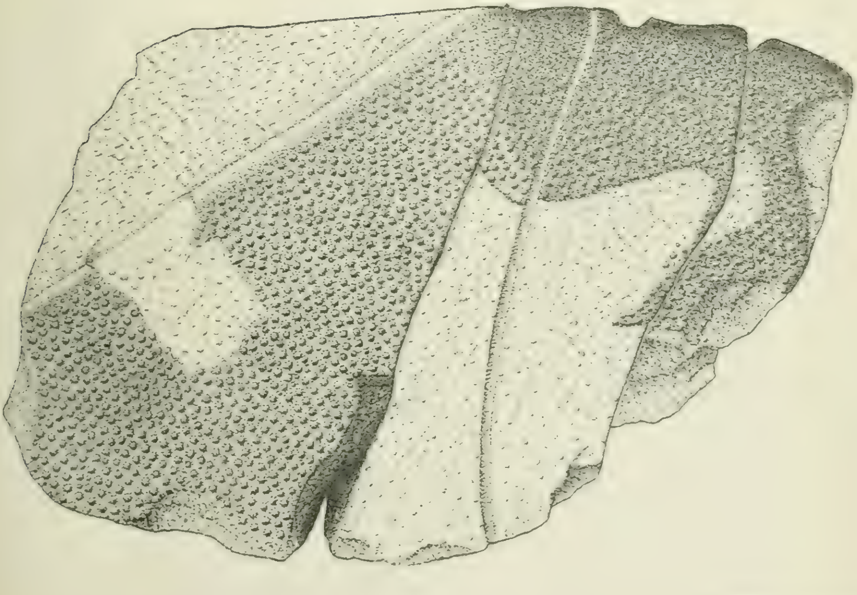

PLATE 4.

Dinichthys (?) *newberryi* Clarke. × $\frac{1}{3}$. Portage Shale; Sturgeon Point, near Buffalo, New York. Weathered plastron and associated fragments. Reproduced from a photograph without retouching.

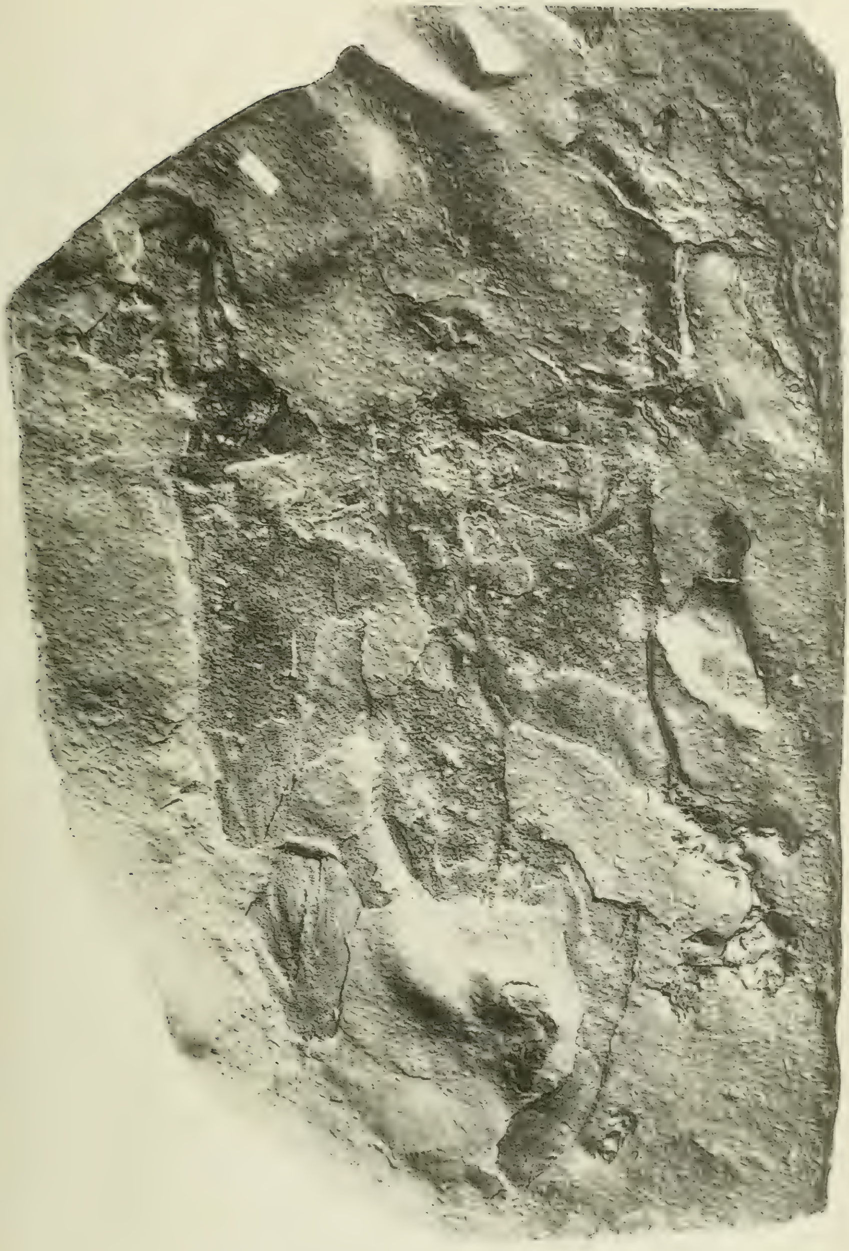

PLATE 5.

Fig. 1. Postero-ventro-median plate of an unknown Dinichthyid species. × $\frac{2}{5}$ (approximately). M. C. Z., Cat. No. 1475. This plate is preserved in counterpart, and a portion of the bone adheres to the opposite side.

Fig. 2. *Dinichthys* (?) *bohemicus* (Barr.). × $\frac{1}{3}$. Middle Devonian (Étage Gg^1); Chotec, Bohemia. M. C. Z., Cat. No. 1376. Detached dorso-median plate, more highly arched and rounded in outline than that shown in Plate **2**, Fig. 3, but having the same ornamentation. The carinal process is slender, and appears only in section where the matrix has been ground away.

Fig. 3. Dorso-median plate of a young individual representing an unknown Dinichthyid species, seen from the under side. × $\frac{3}{4}$. Cleveland Shale; vicinity of Cleveland, Ohio. Original preserved in Museum of Oberlin College.

Fig. 4. *Dinichthys eifeliensis* Kayser. × $\frac{1}{3}$. Middle Devonian; Eifel District. Internal aspect of right antero-ventro-lateral plate. M. C. Z., Cat. No. 1474.

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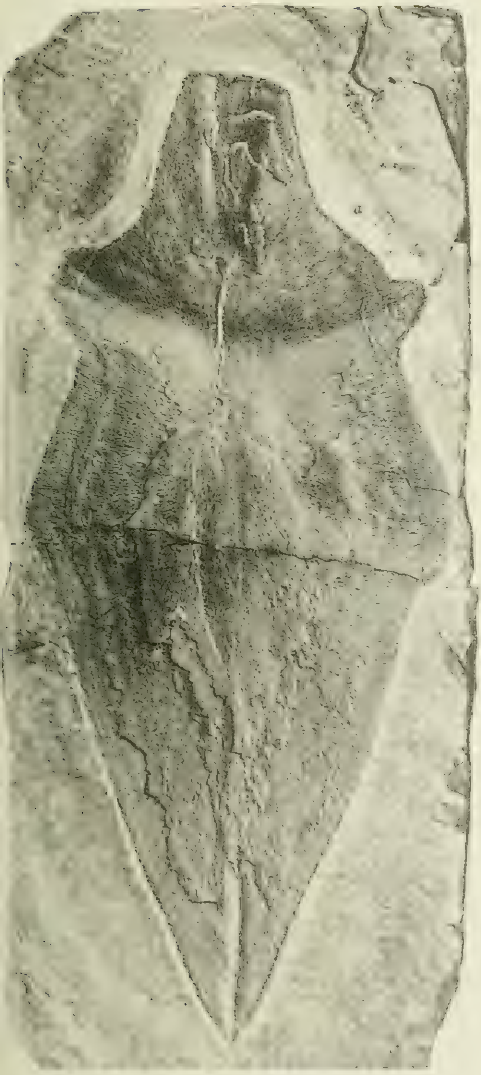

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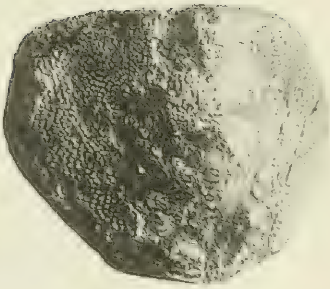

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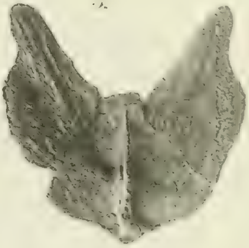

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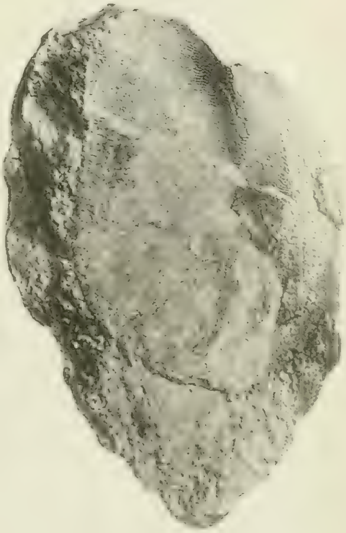

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No. 3. — *Trichonympha, and other Parasites of Termes flavipes.*

By JAMES F. PORTER.[1]

CONTENTS.

1. Trichonympha agilis 48
2. Pyrsonympha vertens 59
3. Dinenympha gracilis 65
4. Gregarinida 65
Papers Cited 67
Explanation of Plates 68

NEARLY twenty years ago Dr. Joseph Leidy ('77) discovered several new and quite distinct species of Protozoa living parasitic in the intestine of Termes flavipes.[2] A few years later he ('81) published an extended account of these strange creatures, accompanied by a large number of drawings illustrating the great variety of forms which they assume. Some of these parasites, to which he gave the name Trichonympha agilis, were so unlike any previously described Protozoa that their discoverer was not entirely certain where they ought to be classed; at first ('77) he regarded them as "probably related with the Turbellaria on the one hand, and by evolution with the Ciliate Infusoria on the other." Later ('81, p. 529), however, he was disposed to view this parasite as having a character intermediate between a ciliate infusorian and a gregarine, but (p. 436) more nearly related to the gregarines.

Since then W. Saville Kent ('85) has made some additional observations on the structure and habits of this parasite from material sent to him by Dr. Leidy, and has also discovered a very similar parasite, to which he gave the name Trichonympha leidyi, in the White Ant of Tasmania.

Besides these studies on Trichonympha, there have appeared descriptions of some other forms which seem to be closely related to this genus. I refer to Joenia, described by Grassi ('85), and to Lydionella, found by Frenzel ('91), both parasitic in the intestine of Termites. The paper by

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. LXXXIV.

[2] Some of these had been previously seen by Lespès ('56); but he alluded to them only briefly (pp. 237, 258) in his memoir. Compare Leidy ('81, pp. 425–428).

Frenzel is especially important, because it gives a careful account of the structural conditions of the genus studied by him, though even he did not make use of sections to ascertain the minuter details of structure.

At the suggestion of Dr. Mark, I began in the autumn of 1895 an investigation of this peculiar and interesting parasite of Termes flavipes, in the hope of being able, by means of more recent methods, — especially sectioning, — to add something to what was already known concerning them. An excellent 1.5 mm. homogeneous immersion by Zeiss has been of much value to me in studying the minute details of structure. In October I captured some of the White Ants, both "workers" and "soldiers," in the woods near Cambridge, and on opening the intestine of one of them found it swarming with the same kinds of parasites that Leidy had discovered in his New Jersey Termites.

1. Trichonympha agilis.

Plate 1: Plate 2; Plate 3, Figs. 24-26.

I have represented in Figures 1 and 2 what seem to me fairly normal and characteristic appearances of a quiescent T. agilis, and in Figure 3 a view of the head end, seen from the anterior pole. My figures should be considered, however, simply as in a measure supplementary to those of Leidy. His observations were so careful and accurate that I have almost no modifications or corrections of his description to suggest; but I shall be able to add something to his account.

Upon seeing one of these peculiar animals, the question immediately arises, Wherefore such a remarkable cloak of cilia? Well developed locomotor organs are the last thing one would expect to find in a parasite whose food is close at hand and whose field of exploration is so limited. With the hope of getting some light on this question, and wishing at the same time to discover, if possible, the situation of the mouth, I experimented by putting living specimens into various fluids; among others, into very much diluted milk. The Trichonymphæ immediately on escaping from the intestine began ploughing their way through the milk corpuscles, passing across the field of the microscope so rapidly that, in order to follow them, it was necessary to keep the slide in constant motion. The various courses traversed by them were indicated by paths cleared of the oil globules. Upon watching their movements, it presently became apparent that the shortest and most anterior cilia were to a very large extent responsible for the motion. The longer cilia, those extending backwards to about the region of the posterior end of the body (Figs. 1, 2) vibrated but little, while the very long cilia that enveloped the posterior half of the animal and reached out far behind (Figs. 1, 2) appeared to be absolutely motionless. These last are not quite useless, however, for I noticed that milk corpuscles began to be entangled among them, and soon afterward long trains of globules were being dragged behind each animal (Figs. 6 and 4). At first I thought this was merely accidental, but after longer observation I came to the conclusion that the cilia actually enfold the globules, for these are gradually drawn in towards the animal, and finally come to lie in close contact with the posterior part of its body (Figs. 4, 5). That the cilia are prehensile in their nature has already been observed by Kent, for he says: "When placed in diluted milk, the animalcules of both the American and Tasmanian species of Trichonympha have been observed by me to assume a fixed condition that has not hitherto been described. An attachment to the surface of organic substances or other convenient fulcra is then accomplished through the medium of the long fascicle of hair-like cilia that are produced from their posterior extremity. These cilia, intersecting one another at a short distance from the body, form a sort of hollow cone, the expanded base of which grasps the selected fulcrum of support after the manner of an acetabulum. This habit of, as it were, anchoring themselves by their long caudal cilia was observed in both the adult and the immature animalcules."

I have observed that Trichonympha may attach itself even to the cover glass by means of its cilia. This evident habit of grasping things by means of the caudal cilia suggested the idea that these cilia might perhaps have the function not only of attaching the animal to the host, but also of procuring food ; however, I must acknowledge that it appeared highly improbable that these seemingly motionless cilia, which clothe and tightly invest the animal, could have a function which ordinarily requires so much activity ; furthermore, I had been unable thus far to find any mouth opening. Kent in his article says (p. 271) : "An important point that was left undetermined by Dr. Leidy respecting the structure of Trichonympha relates to the precise position of the oral aperture. The bodies of the animalcules are almost invariably filled with fragments of the woody débris devoured by their hosts, the White Ants, which shows that their sustenance is taken into their body in a solid state, and is not simply absorbed in the fluid form, as occurs with the group of the Opalinidae. A prolonged observation of living examples of the American species remitted me by Dr. Leidy, and likewise of the Tasmanian type here introduced, has resulted in my determining that a distinct oral aperture is developed upon one side of the body at a short distance only from the apical extremity. This orifice takes the form of a transverse slit, and is followed by a narrow œsophageal tract which opens into the capacious digestive cavity that occupies one half or two thirds of the posterior region of the body. The plan recommended by Dr. Leidy for observing the vital phenomena of these animalcules is to empty out the intestine of the White Ant containing them into a little white of egg. I also have found this material favorable for their observation, but have gained an additional insight into their life history by employing in a like manner thinly diluted milk. In this medium they not only live for a considerable time, but meet with abundant nutriment, their pharynx and digestive cavity being frequently found densely packed with its component corpuscles after their immersion in this fluid for a short interval."

Unfortunately, Kent does not give any figures, and I have been unable to discover in the living animals the mouth he describes. However, the existence of such a structure could, I imagined, be easily determined by means of sections. These I endeavored to procure by sectioning the whole alimentary canal of the Termes, hoping in this way to obtain some sections of Trichonympha in a direction favorable for settling this point. I was not disappointed.

To my astonishment I found that the small intestine was completely packed with animalcules, and among them hundreds of Trichonympha; these, however, were not promiscuously distributed through the parasitic mass, but were, as a rule, excluded from the periphery of the intestine. This position, of course, precluded the possibility of their attaching themselves directly to the wall of the host's intestine.

The sections of Trichonympha thus obtained revealed absolutely no trace of such an oral aperture as that described by Kent. They did show, however, an interesting condition of affairs, which I think may perhaps account for the presence of the numerous fragments of ligneous fibre and other food particles so often found within the body, without necessarily supposing them to have entered through a persistent mouth. In many of the cross sections of the posterior half of Trichonympha I observed deep folds of the body wall; these almost invariably contained cilia, doubtless engulfed at the time of the folding (Plate **2**, Figs. 9, 10, and 14). Particles of wood fibre were also seen entangled among the cilia in these folds (Fig. 10, *fbr. lig.*). I think we have in this condition an explanation of the mystery. Cilia entangling particles of woody fibre become surrounded by a deep fold of the posterior part of the body. The most of the cilia are probably afterwards withdrawn from the fold, but the lips of the fold become so closely applied to each other (Fig. 14), that the ligneous particles are left behind in the depths of the fold. I believe that the lips of the fold afterwards fuse together, that the walls of the infolded portion then disappear, and that the food thus finally becomes entirely enclosed in the body protoplasm of the parasite. The condition of the body wall at *a* in Figure 14 seems to indicate that the wall is there in process of disintegration or dissolution.

This is certainly a remarkable method of feeding for a ciliate infusorian; but I see no escape from the conclusion that solid food material never enters the animal in any part of the anterior nucleus-containing portion of the body; for of the hundreds of specimens that I have examined, both living and dead, none have ever shown solid particles of food in the anterior region, whereas the absence of ligneous matter from the posterior part of the body is a condition rarely met with. It seems highly improbable — to say nothing of the absence of any trace of a permanent oral structure — that solid food should pass through this anterior region so quickly that not a single case of its passage, or of its presence in this part, should have been discovered by any one of those who have studied these parasites.[1] But besides this, it is to be noted that the wall of the whole posterior part of the body is thin and exceedingly delicate, so that it would not present any great barrier to the entrance of foreign particles. It disintegrates so readily that I have seen this portion of a living animal go to pieces completely and disappear, while the anterior half, bearing the cilia, continued to swim around.

For the sake of convenience in description, I shall recognize in Trichonympha three regions (compare Plate **2**, Figs. 13, 15, 7): first, an anterior nipple-like part, which is quite sharply separated from the following region; secondly, the middle or bell-shaped part, the axial hinder portion of which usually projects a greater or less distance into the following or third part, and always contains the nucleus. These two parts together have been called by Leidy the "head." Thirdly, the posterior part, to which Leidy gave the name of "body."

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[1] It is true that Kent speaks of seeing the "pharynx" and digestive cavity densely packed with milk corpuscles; but while this is the case in the posterior portion of the body, I have never seen milk globules or other particles of food in any part of the organism that could be likened to a pharynx.

Frenzel ('91) likewise was unable to find direct evidence of the existence of a mouth opening in Leidyonella. Although he inclined to the opinion that it was located at the anterior end of the elongated neck-like region, he admitted the possibility that it might be located elsewhere. Grassi ('85), too, was equally unsuccessful in locating the mouth in Joenia, although in this genus likewise the presence of particles of woody fibre in the body shows that solid food is taken in.

I begin with the anterior region, which I have found to be of rather complicated structure. To aid in the description, I have made several large semi-diagrammatic sketches (Plate **2**, Figs. 7, 8, 11, 12, 17). Figures 7 and 8 are intended to represent sections not thicker than the space between two successive longitudinal rows of cilia.

The *nipple-like part* of Trichonympha is, as the name which I have given it implies, a conical, more or less elongated protuberance at the front end of the parasite. According to its state of contraction it is one half, two thirds, or even more than two thirds, as thick at its base as it is long. The anterior end is evenly rounded or sometimes more pointed. Seen in profile its outline at the posterior end usually passes gradually into that of the middle part, but at times it appears sharply separated from this part by a deep constriction. Deep focusing and especially longitudinal sections show that the separation is more complete than superficial focusing would lead one to suppose.

The "nipple" consists of a cylindrical, or slightly tapering, rod-like axis (Plate **2**, Figs. 7, 8, 18, *ax.*), composed of finely granular protoplasm, and one or more enveloping layers unlike in structure. The anterior end of the axial rod is expanded into a knob-like enlargement (Figs. 7, 8, *tub.*), the anterior surface of which has a conical (Fig. 7), or more commonly a hemispherical (Fig. 8) form. The rod is narrowest a little in front of its middle, and thence increases in thickness very gradually both toward the knob and toward the "bell." The protoplasm of the axial rod is continuous behind with the granular protoplasm which occupies the axis of the "bell," and its surface appears to be differentiated into a thin membrane. This protoplasmic axial rod is surrounded by two, and possibly sometimes by three, well differentiated layers of formed substance (Fig. 7, *st.′*, *st.‴*; Fig. 8, *st.′*, *st.″*, *st.‴*). The middle layer often appears as though caused by an accidental separation between the outer and inner layers, but it is of so common occurrence that I do not feel able to declare positively that it is merely an artificially produced space.

The anterior extremity of Trichonympha terminates in a colorless translucent cuticular cap (Figs. 7, 8, *pil.*), which stains only slightly at most, and frequently not at all. The centre of the cap covers the anterior expanded end (*tub.*) of the rod-like protoplasmic core, and its margin rests on the anterior sloping surface of the outer layer (*st.'''*), while the anterior end of the inner layer (*st.'*) is covered by the expanded knob-like portion (*tub.*) of the protoplasmic core (Figs. 7 and 8).

The whole of this portion, forming the nipple-like projection of the anterior extremity of the animal, is very active in the living creature; it is constantly in motion, turning from side to side, and, as it were, nosing its way through the crowd of its associates.

The axial rod (Figs. 7, 8, *ax.*) is apparently the only means of union between this nipple-like part of the animal and the bell-shaped region, for a fissure (Figs. 7, 8, *fis.*), encircling the base of the nipple, penetrates the layers surrounding the axis, thus severing all other connection. Behind the fissure, what seem to be continuations of the outer and inner layers of the nipple are carried backward over the bell-shaped region, i. e. over a little less than one third the length of the animal. A middle layer never appears in this region, a fact which makes it seem probable that such an appearance in the nipple region is due merely to a space between the inner and outer layers. Since the enveloping layers are so much alike in the nipple- and bell-shaped regions, I shall not attempt to give a separate description of them in each region, but proceed at once to state what I have to say about these layers for the whole "head" region.

The inner layer stains only slightly, if at all. From the fissure backwards, as far as it extends, it is marked by fine lines perpendicular to the surface. This appearance is due to the cilia, which penetrate both the enveloping layers. The same structural condition probably exists in front of the fissure, although it was not possible, owing to the small diameter of the nipple-like projection (about 6 μ) and the thickness of my sections (3.3 μ), to detect any striations.

The cilia arise from the granular protoplasm, at the deep surface of the inner layer, which they traverse, and thus give a striated appearance (Fig. 16, *st. str.*). They are of about the same refractive power and stainability as the outer layer, and consequently I have not been able to trace them through that layer; but I think that their passing through it is hardly questionable. The arrangement of the radial striations of the inner layer, which I believe to be due to the cilia, is best made out from tangential sections of the bell, where their cut ends appear as dots. The dots are placed in quincunx order, much as shown in Fig. 20. This arrangement gives two series of diagonal rows of dots crossing each other nearly at right angles and making angles of 45 degrees with the longitudinal axis of the animal. Secondary rows, both parallel and perpendicular to the longitudinal axis, though less regular than the oblique ones, are easily recognizable. Owing to the surface of the bell being curved, the arrangement in quincunx is not as evident as I have represented it diagrammatically in Figure 20, but has more the appearance shown in Figure 19, where the oblique and transverse rows are somewhat curved, and the longitudinal ones diverge slightly as they pass backwards.

The outer layer (Fig. 7, *st.‴*) is composed of a series of ridges, or, more properly speaking, plates. These plates, cut crosswise, are shown in Figure 16 (*st.‴*), which represents a transverse section through the middle of the bell-shaped ciliated portion of the body, about in the place indicated by the line 16–16 in Figure 15. The plates are seen more clearly in the diagrammatic cross section shown in Figure 17, *st.‴*. In surface views of the animal each of the plates of the nipple appears to be split into two at the region of the fissure (Fig. 11, *fis.*); this, however, is only an optical illusion. Although the plates of the bell-shaped part are twice as numerous as those of the nipple-like part, there is no continuity between the two sets, the appearance of splitting being due to the overlapping of the anterior set over the posterior one. The nature of this overlapping (Fig. 12, *fis.*) may be seen in optical longitudinal sections. The plates of the outer layer coincide with the longitudinal rows of cilia. Their inner edges are slightly serrated (Fig. 8, *csp.*), owing to a slight inward prolongation of the plate wherever a cilium in passing through meets it. It is this condition which causes the interrupted appearance of the plates seen in tangential sections (Fig. 20, *csp.*).

The *bell-shaped region* is generally sharply marked off from the anterior or nipple-like part by a deep constriction (Plate **1**, Figs. 1–6); but sometimes there is a more gradual transition (Plate **2**, Figs. 7, 8). The boundary between the "bell" and the "body" is ordinarily marked by a deep constriction (Plate **1**, Figs. 1, 6), or a shoulder-like projection of the "body" beyond the outline of the "bell" (Plate **2**, Figs. 7, 15). The place of this constriction may for convenience be called the lip of the bell, though the pendant central mass of the protoplasm of the bell containing the nucleus often projects far behind this rim or lip. When the animal is at rest, the bell is of fairly regular and symmetrical form (Figs. 13, 15), but the extreme mobility of the whole head region causes it when in action to take a great variety of shapes (Plate **1**, Figs. 1–6).

The protoplasm of the bell is differentiated into two distinct kinds, a coarser and a finer. The coarsely granular protoplasm is situated chiefly in the anterior portion of the bell (Fig. 7, *pr'pl.*), but it is also continued backward along the surface, and likewise forms a pendant-like structure in the axis of the bell (*pr'pl. ax.*, Figs. 7, 13, 15). It stains a little darker than the finer protoplasm which occupies the rest of the bell, but the transition between the two kinds is not very abrupt.

Extending backward from the lip of the bell is a coarsely granular protoplasmic partition (Fig. 7, *st. gran.*), continuous with the coarsely granular protoplasm of the surface of the bell, and marking the boundary between the "head" and the "body" of the animal. It has the form of a hemispherical bowl, at or near the bottom of which is situated the nucleus. Although I have been unable to discover in connection with this granular partition the existence of any fine membrane serving to completely separate head and body, yet the constant relation of the nucleus to this granular layer proves the latter to be substantially a permanent boundary between these two regions of the animal. In cross sections of the animal in the region of the nucleus (Figs. 21, 23; compare the position of the lines 21–21 and 23–23 in Fig. 15), this partition gives rise to a kind of radiation, which seems to emanate from the nucleus. This appearance might be produced if the bowl-shaped layer of granulations were corrugated or thrown into radiating folds; but I believe it is due instead to a regular alternation in the *thickness* of radiating portions of the bowl. As seen in cross sections (Figs. 21, 23) this bears a slight resemblance to the crown of rods (bastoncelli) figured and described by Grassi ('85, p. 236, Figs. 1, 2, 6), as nearly enveloping the nucleus in the case of Joenia annectens; but the fact that the bastoncelli have a more precise form, being short club-shaped and curved, as well as the fact of their not being limited to a single zone, seems to me to preclude the possibility that these two structures are homologous.

The nucleus (Fig. 7, *nl.*) is situated in the anterior or "head" portion of the animal, a little posterior to the constriction at the surface which marks the transition from the "bell" to the "body." It lies wholly within the bell-shaped portion, however, and is generally surrounded by a thin sharply defined nuclear membrane. I have almost invariably found the chromatin broken up into chromosomes of varying size and shape, and without definite arrangement.

Very frequently the nucleus is invested with an immensely thickened membrane (Plate **2**, Fig. 22). This nuclear envelope consists of a clear homogeneous substance, which stains in eosin, but not in haematoxylin.

I have found several stages which I believe lead up to this condition. Apparently the substance which is destined to envelop the nucleus first collects along the partition separating the body from the head of the animal (Fig. 13). Possibly the formation of this thick envelope is preparatory to the production of the spores.

The posterior or body half of the animal is principally occupied by a highly vacuolated protoplasmic mass (Fig. 7), which has usually reached the state of a coarse reticulum. In this reticulum large pieces of wood fibre and spores of fungi are frequently found embedded. This central protoplasmic reticulum is completely surrounded by a granular protoplasmic wall (*st. gran.′*, Figs. 7, 13, 15), which is continuous in front with the granular partition separating the "head" from the "body."

The granular wall is not very thick, and passes on its inner surface rather gradually into the protoplasmic network; but it is more sharply defined on its outer surface, though even here the transition to a rather thick cortical layer (*st. ctx.*, Figs. 7, 13, 15) immediately outside it is not very abrupt. This cortical layer is composed of finely granular almost homogeneous protoplasm, and is of nearly, though not quite, uniform thickness. Its average thickness is about the same as that of the inner layer enveloping the bell.

The surface of the "body" appears to be traversed by nearly equidistant lines, which have a slightly spiral — left-handed or læotropic — course (Plate **1**, Figs. 1, 2). These lines appear to be continuous in direction with the innermost set of cilia, which cross one another at the posterior tip of the body, and in fact the lines are in my opinion due exclusively to the presence of these cilia, which are closely applied to, but are entirely free from, the wall of the "body." Frenzel's description of the condition in Leidyonella is certainly not applicable here. Frenzel ('85, pp. 306, 307) maintains that in Leidyonella the rigid cilia arise at or near the anterior end of the body, but that, instead of being free throughout their whole length, they are fused with the peculiar cuticula which covers the body, causing ridges, which have a slightly spiral course (he does not say whether right or left, and his figures are noncommittal), and that they become free only as they project beyond the posterior extremity of the body. These ridges are stated to be much more prominent in the anterior than in the posterior part of their course. But, whatever may be the condition in Leidyonella, the spiral markings in Trichonympha are not traceable forward any further than the boundary between "body" and "bell," and they are not due to confluence of cilia with the wall of the body of the parasite.

The questions of reproduction and development in Trichonympha, though interesting, are very difficult, and I shall not be able to say much on them.

I have chanced upon three individuals, which I at first thought to be stages of division (Plate **3**, Figs. 24–26), but having seen only these three, and these being all from the same host, I am now inclined to think that they are simply abnormal forms. But whether these are normal or abnormal, I believe that division must be of rare occurrence.

Leidy has figured several forms (Plate 51, Figs. 11–20), always found associated with Trichonympha, which he thinks may be their young; but I believe that not all the forms referred by Leidy to Trichonympha can be the young of that genus. Perhaps, indeed, none of them are. Those which seem to me to present the best evidence of being the young of Trichonympha are shown in Plate **3**, Figs. 27–29 (compare also Leidy's Plate 51, Fig. 11). These individuals possess a nucleus situated in about the same relative position as that of the adult Trichonympha, and are provided with long cilia. The cilia begin at the base of a smooth knob (Fig. 29), with which the anterior end of the animal terminates, and follow from there the course of deep spiral grooves that have the direction of the threads of a right-hand screw, not, as one might infer from Leidy's Figure 11, that of a left-hand screw. The grooves are much closer together on the anterior than on the posterior portion of the parasite, and consequently, as in the adult Trichonympha, the cilia are much concentrated into this region. Again, as in the adult Trichonympha, a bunch of long cilia trails out behind the parasites of this type. Moreover, the anterior cilia alone are used, as in the adult Trichonympha, for locomotion, the body often remaining during locomotion perfectly rigid and the posterior cilia quiet.

This spring (1896) I have noticed a great many specimens of this parasite with a very much enlarged, apparently swollen, anterior knob (Fig. 28); but what this condition signifies I have been unable to determine.

Notwithstanding these several points of agreement, there seem to me to be almost insuperable obstacles to assuming that there is a genetic relation between the two forms. Chief among these is the pronounced dexiotropic course of the spiral groove and accompanying bands of cilia in the supposed young; whereas in the adult Trichonympha the bands are *longitudinal* and are limited to the anterior or bell-shaped part. A direct conversion of one of these conditions into the other seems to me highly improbable, while the obliteration of one and a substitution of the other would amount to nothing less than a metamorphosis, none of the steps in which have been observed.

Another point of difficulty is the entire absence in the supposed young of any partition separating the nucleus-bearing anterior portion of the organism from the posterior portion.

The other forms, resembling those which Leidy thinks may also be young of Triconymphæ, I have represented in Figures 30–32, 35–39, and 42–44. I can see no sufficient reason, however, for supposing them to be young Trichonymphæ. The nucleus of these forms is situated at the extreme anterior end of the body. The anterior tip terminates in a rounded projection, but it has not the form of the knob seen in Figures 27 and 29, and a comparison with the cap seen in adult Trichonymphæ is more difficult in this case than in that of the forms last described. The cilia are of very nearly equal length over the entire body. They are arranged in bands running spirally around the animal, and the spirals run in the same direction (dexiotropic) as in the forms we have just been discussing.

There are, however, so many points of difference between these two kinds of supposed young parasites as to render it probable that they are not connected with each other genetically any more than they are with Trichonympha. It will be observed not only that the nuclei are differently situated in the two forms, but also that in those shown in Figures 30–32 and 35–38 the interval between successive bands of cilia remains nearly constant throughout the entire length of the animal, quite unlike the condition obtaining in the other forms.

This form is also found in a great variety of sizes (Figs. 30, 31, 35), the largest being considerably larger than the individuals of the other form represented in Figures 27 and 28. The shape of the animal is characteristic, being in the living condition long and slim. Figures 37, 39, and 42–44 represent living specimens. Figure 38 shows one that died in normal salt solution. Figures 30–32, 35, and 36 represent the shapes they assume when killed with corrosive sublimate. Their method of locomotion also serves to distinguish them from the forms which I have last described, for they often move, independently of ciliary activity, by changes in the form of the whole body (Figs. 39, 42, 44), — sometimes with the wriggling, squirming motion of a worm, at others, swelling out in places to almost double their average diameter, and then slowly contracting their body-wall (Fig. 44), they produce a kind of peristaltic motion, which may aid in locomotion. The smaller ones (Fig. 43), when travelling very rapidly in a straight line, revolve around the longitudinal axis, their bodies changing form little or not at all. This rotation is undoubtedly due to the spiral arrangement of the cilia, but the constant motion of these organs makes it impossible to discover in living specimens what the arrangement of the cilia is.

The bodies of these worm-like animalcules (Figs. 30–32, 37–39, 42–44) are invariably filled with great numbers of large protoplasmic granules; this is not the case with any of the other parasites.

It seems to me that the characters of this form are sufficiently definite and different from those of the other forms described to allow one to consider them the representatives of another species.

2. Pyrsonympha vertens.

Plate 3, Figs. 33, 34, 40, 41; Plate 4; Plate 5.

Pyrsonympha in its mature state is much larger than Trichonympha. Either the parasites found in the vicinity of Cambridge attain a greater size than those studied by Leidy, or else this author failed to see the largest individuals, for the longest specimen seen by Leidy measured only 160 μ, whereas the one which is shown in longitudinal section in Figure 33 (Plate **3**) is 275 μ long, exclusive of the peduncle; this being a large, but not an exceptionally large individual.

Pyrsonympha, like Trichonympha, evidently feeds on solid food, so that the question again confronts us, How does this food enter the body? Sometimes the whole posterior portion of the animalcule is filled with fragments of wood fibre (Fig. 34). These fragments are often of considerable size. I have seen, within the posterior part of the body, a single rectangular piece so large that it touched both sides of the body, and extended anteriorly almost to the nucleus. Surely, a mouth large enough to swallow such a portion of food must be recognizable; but I have been unable to discover any aperture whatsoever in the body-wall of the animal.

Pyrsonympha is usually more or less club-shaped, the relative proportions of length and thickness, and the particular form, being of course dependent on the degree and nature of its contraction (Plate **3**, Figs. 33, 34, 40, 41; Plate **4**, Figs. 45, 51, 53, 55). In the adult condition it appears always to be attached to the wall of the host's intestine, a fact which Leidy, strangely enough, seems to have entirely overlooked. The attachment is by means of the narrower end, which is prolonged into a sort of homogeneous stalk or peduncle, having only a slender connection with the main portion of the parasite. The peduncle is from $1\,\mu$ to $1.5\,\mu$ in diameter, and may attain a length of at least $75\,\mu$. It is deeply embedded in the epithelial wall of the host's intestine. I am not certain that I have been able to trace it to its end, and do not know if there is any specialized structure at the end; consequently I cannot state the possible maximum length. It is usually of almost uniform calibre throughout the most of its length. The region near the point of attachment, however, often shows a spindle-shaped enlargement (Plate 4, Fig. 45). There is invariably a spheroidal structure that I have called the knob or tubercle (Figs. 46, 47, *tub.*), which serves as a means of connecting the peduncle with the rest of the body; when an artificial separation between body and peduncle takes place, the tubercle may remain attached to either part, but it usually separates from the body (compare, however, Fig. 47). The tubercle is somewhat thicker, and becomes much more deeply stained, than the peduncle; it is homogeneous and highly refractive.

The attached end of Pyrsonympha is that which Leidy has called the anterior end. Accepting this designation simply as a convenience in description, it may be said that the free posterior part of the parasite projects with a rounded end into the lumen of the host's intestine. The body of the parasite, from the narrow tuberculate part to the free rounded end, looks like a thin sac.

The body-wall itself is frequently excessively thin, and in places the body seems to be almost naked and amœboid in its nature. The slightest pressure of an object on its surface would cause it to enter the substance of the body. I believe that something of this kind is represented in Figure 40 (Plate 3); at any rate, in this case a particle of wood fibre was found about three fourths engulfed by the animal; whether the fragment was accidentally forced into the body, or whether the animal was taken in the act of ingesting it for food, I am unable to say. The parasites, of which this was one, had been removed from the host for about an hour when I discovered this individual. During the three or four minutes that I watched this one no change took place, and at the end of that time it was dead. So it is still only a matter of conjecture that Pyrsonympha engulfs its food by the exceedingly mobile posterior portion of the body.

However that may be, the body-wall is so thin in all regions as to make the condition noteworthy. There is no place where its thickness is sufficient to allow it to be readily measured. In fully grown individuals the body is only sparsely covered with cilia, and portions of the surface seem to be entirely destitute of them. When present they are scattered irregularly, apparently without relation to the contractile cords of the body-wall. The young, as we shall see later, are provided with a coat of abundant cilia uniformly distributed.

The body-wall is not without further differentiation, for at regular intervals it is marked by darker lines, which have the appearance of thickenings of the wall, or of separate cord-like structures applied to its inner surface. These are really contractile cords, which arise at the knob-like structure of the anterior tip of the parasite where it joins the peduncle. These cords are usually grouped together at the anterior end of the body, so that a portion of the surface is quite bare of them (Plate **4**, Fig. 51 *a*). They pass backward in a slightly spiral direction (læotropic), leaving between one another equal spaces. As a rule, each cord can be traced to the posterior extremity of the animal, and thence back again on the opposite side of the animal to the anterior end; but sometimes the cords apparently terminate in cup-like depressions in the body-wall, which resemble pock-marks, being outlined by coarse granular protoplasmic rings (Fig. 51, *ann.*). The cords are frequently so superficial that in profile views of the animalcule they are seen to cause the surface to project in the form of ridges. In some individuals there is to be seen in the middle of the space between two successive cords another and much finer line (Plate **4**, Figs. 47, 54) running parallel with them. This narrower line or cord is apparently embedded in a more or less clear homogeneous substance, while the larger cords are surrounded by coarse granular protoplasm. In other cases the larger cords occupy the clear areas, and midway between them are sharply marked lines of coarsely granular protoplasm, which stains more deeply than the rest of the protoplasm (Fig. 51).

In living specimens these cords keep up an incessant undulatory motion, producing an effect which very closely resembles bands of vibrating cilia The body of the adult, however, is generally quite bare of cilia, but when it is ciliated, the cilia are, as I have said, scattered promiscuously over the body, irrespective of the contractile cords.

The contents of the sac-like body are finely and rather uniformly granular, and not very thick or viscid, and there are appearances of vacuolation in them.

The nucleus of Pyrsonympha is a large pear-shaped or sometimes oval body, generally situated at about one fourth or one third of the distance from the anterior or attached end to the posterior end, and its more pointed extremity is turned toward the attached end of the animalcule. It always contains a nucleolus (Plate **4**, Fig. 47, *nll.*) at its larger end, and frequently it is highly vacuolated at its anterior end. Figure 52 (Plate **4**) represents a cross section of a Pyrsonympha through the nucleus, showing its position and that of the flagellum (*fg.*) in relation to the wall of the body. The nucleus varies considerably in shape; sometimes it is very much attenuated (Fig. 50), and at others almost spherical (Fig. 53, *nl.*).

Within Pyrsonympha is a lash-like filament or flagellum (*fg.*), as I shall call it, which is by far the most remarkable structure of this parasite. In the living specimen it is in constant motion, great waves passing from the attached to the opposite end of the animal, often giving it the appearance of a revolving polygon inside the animal. Leidy says, "The motion of the undulating cord and of the animal together impressed me with the idea of a snake in a bag, making its presence obvious in active contortions." The effect of this flagellum is not unlike that of a churn, for it keeps the contents of the sac-like body, including the food, thoroughly stirred up.

The flagellum is of nearly uniform thickness throughout the most of its length, and, as cross sections (Fig. 52) show, is oval in section; its diameter varies with the state of contraction, but averages about 1.5 μ by 2 μ. Near its anterior end, where it joins the peduncle by means of the darkly staining tubercle, it sometimes becomes very much attenuated (Plate **4**, Fig. 46). I am not certain, however, but that this may be due to abnormal tension induced by the increased activity of the flagellum when the parasite is put in normal salt solution. However this may be, the posterior portion of the flagellum tapers off very gradually, finally becoming very fine at its posterior end (Figs. 45, 53, 55).

Throughout the most of its length it is quite free from the body-wall, and moves about with vigorous strokes in the most unexpected manner. It is, however, attached to the body-wall at or near the posterior end of the parasite, as well as at the region of the peduncle. But quite frequently it seems to break loose from this posterior place of attachment, — perhaps owing to a too violent whipping about caused by the stimulating effect of the salt solution, — and then it sometimes projects posteriorly in the form of a tail-like appendage. This caudal appendage is surrounded by a layer of protoplasm, which has considerable thickness at its base, but becomes reduced to a condition of great tenuity (Plate **3**, Fig. 34) at its tip. It flaps backward and forward very violently with every undulation of the flagellum.

Leidy ('77, p. 437) says of Pyrsonympha, "Sometimes too it appears terminated by a caudal appendage of variable form and length, but this has seemed to me to be a production resulting from change due to dissolution." It does not appear from anything said elsewhere, or from his drawings, that he connected the presence of this caudal appendage with the vibrating cord.

The method employed in removing from the host the living animalcules for study has proved to be important, for it is to this that I owe the discovery of the peduncle previously described. Leidy speaks of gently pressing the intestine of the host, and thus forcing out the parasites. Instead of doing this, I removed the intestine into normal salt solution and on the slide teased it into pieces with needles. In this way of course many fragments of the intestine were found mingled with the parasites. These were frequently covered with Pyrsonymphæ, so closely packed together that they looked at first sight like large epithelial cells. Each of the parasites was attached to the fragment of the intestinal wall by a long filament (Plate **4**, Fig. 45). I think that Leidy saw this filament or peduncle, as I have already called it, for he says ('77, p. 438), "In the process of dissolution of the animal, the undulating cord [flagellum] often appears to project to a variable extent from the narrower end of the body"; but he did not recognize that this projecting part was a means of attachment, for on forcing Pyrsonymphæ from the intestine the most of this peduncle must invariably have been broken off. Normally, I believe, all mature Pyrsonymphæ are attached to the intestine by means of this peduncle.

The few evidences of reproduction which I have observed relate to the conditions of the nucleus or the size of the individuals. I have observed nuclei in what I believe to be various stages of division (Plate **4**, Figs. 48, 49, 55). This shows that probably reproduction by division takes place occasionally. Perhaps Figure 53 represents an individual recently formed in this way; the presence of the nucleus in the posterior portion of the parasite certainly points to that conclusion. Individuals produced by the division of a large adult Pyrsonympha should of course resemble the adult form in the almost total absence of cilia, and also in the possession of a flagellum. It therefore seems safe to assume that almost all unusually small Pyrsonymphæ possessing these qualities (Plate **5**, Figs. 62, 64) were recently formed by division.

Besides young of this type, there are found swarms of immature Pyrsonymphæ with essentially different characteristics. These are, for example, profusely covered with fine, short cilia of nearly equal length (Plate **5**, Figs. 58, 61, 63). Apparently, the flagellum is frequently wanting in these forms, or at least cannot be distinguished (Figs. 57, 63). The superficial muscular cords exist, but take a longitudinal course as often as a spiral one (Figs. 57, 61). Sometimes they are distributed over only a part of the animal (Fig. 61). The nucleus of these small individuals resembles that of the adult, but is situated at the extreme anterior end. If, therefore, it were not for the presence of the flagellum and peduncle in some of these forms, we should be quite unwarranted in supposing them to be in any way related to Pyrsonympha. As it is, however, I think there can be no doubt of the relationship. The flagellum and peduncle are both absent in some forms (Figs. 59, 60, 65) which I take to be the earliest known conditions of this parasite.

I have come to the conclusion that the flagellum of Pyrsonympha is merely a differentiation of one of the superficial muscular cords. We may conceive that the cord which is destined to become a flagellum, after becoming larger, stronger, and more active than any of the other cords (Plate **5**, Fig. 61), simply splits off from the inner surface of the body-wall, remaining fixed only at its two extremities; thus it enjoys free play for all its peculiar undulations.

The peduncle is apparently a slow-growing structure. In sections of the intestine one often finds young parasites in closely packed masses, lining considerable portions of the intestinal wall (Plate **5**, Fig. 56). Their anterior ends lie very close to the intestinal epithelium, thus showing that the peduncle is still very short. The young here referred to (Plate **5**, Fig. 56) are not more than one third or one fourth as long as the adult parasites shown in Figure 45 (Plate **4**). The deeply stained body which is to be seen at the anterior tip of even the youngest individuals (Fig. 56) is the knob-like structure or tubercle of the adult, from which the peduncle arises.

In their activity the young far exceed the adults, for besides the undulation of the muscular cords, the animal is constantly changing its shape. Figures 59, 60, and 65 (Plate **5**) represent different shapes, taken by the same individual in the course of a few minutes.

It is of interest in this connection to note the effect of these parasites on the intestine of the host (Plate **5**, Fig. 56). The epithelial lining is very much indented. The peduncles force their way between the cells, reaching sometimes almost to the underlying muscular layer. The cells themselves are often reduced in size, but otherwise apparently perfectly healthy. It is a mystery how the host can support such a vast number of parasites, unless they in turn are in some way of benefit to it.

3. Dinenympha gracilis.

Plate 6, Figures 66–72.

I have found it almost impossible to draw any sharp line of distinction between Dynenympha and the young of Pyrsonympha; in fact I doubt very much whether Dinenympha should be considered as anything else than a very early stage of a developing Pyrsonympha.

Dinenympha never possesses a flagellum or a peduncle, although at the anterior tip of the animal there is frequently a deeply stained body resembling the tubercle of Pyrsonympha. The body of Dinenympha is long and slim, slightly flattened on one side, and generally twisted with one or two dexiotropic turns. Running parallel with this twist, but upon the convex side only, there are from seven to nine muscular cords, resembling those of Pyrsonympha; but they often cause the surface to project much farther than is usual in Pyrsonympha, giving the animal a fluted appearance. This is shown in Figures 69 and 70 (Plate 6), which represent the upper and lower surfaces respectively of the same individual. Similar views of another individual are shown in Figures 71 and 72.

The animal is generally almost devoid of cilia, except for a tuft at the posterior end (Figs. 67, 68), or occasionally a few cilia at both extremities (Figs. 66, 69). Sometimes, however, it is thinly ciliated all over (Fig. 72). I think Leidy must have mistaken the undulatory motion of the muscular cords for the vibration of bands of cilia, for I have found that individuals with abundant cilia are rare.

The nucleus is situated near the anterior extremity of the parasite; it is oval and homogeneous, or finely granular, and sometimes (Fig. 66) shows a single darker structure like a nucleolus. The nucleus varies in size from $9 \times 5.5\,\mu$ to $5.5 \times 3.6\,\mu$.

The motions of the living Dinenympha are exceedingly interesting, but Leidy has amply described them.

Dinenympha, like its companion parasites, lives on solid food; but it possesses no discoverable oral aperture.

4. Gregarinida.

Plate 6, Figs. 73–76.

Leidy ('81, p. 441) speaks of having only once noticed a small Gregarine among the other parasites of Termes. I have, however, found Gregarines very common in some hosts. They are found, almost without exception, in the anterior portion of the small intestine only. Sections through this part often reveal great numbers of cysts (Plate **6**, Fig. 75). They belong to the Polycystidea. Figure 73 (Plate **6**) shows a very characteristic appearance of a living specimen, and Figure 74 that of one filled with sporocysts.

In sections (Fig. 76) the protomerite (*pr'mer.*) is seen to be compactly filled with protoplasm, the anterior half of which stains more deeply than the rest. The posterior half appears to be made up of globules somewhat flattened by mutual pressure. In living specimens the anterior portion of the protomerite is quite transparent, being free of all coarse granules (Fig. 73).

The deutomerite (Fig. 76, *deu'mer.*) is generally only loosely filled with a coarse protoplasmic network. It contains the large, round nucleus, generally situated quite centrally. Within the nucleus is always to be found a single large deeply stainable nucleolus.

In conclusion, I wish to express my very deep indebtedness to Dr. Mark for whatever there may be of value in this paper. The work was taken up at his suggestion, and carried on under his very kind and careful supervision.

Cambridge, May 12, 1896.

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EXPLANATION OF PLATES.

All the figures, with the exception of those of Plate **2**, were outlined with the aid of an Abbé camera lucida.

The high magnifications were obtained mostly by the use of a Zeiss 1.5 mm. apochromatic homogeneous immersion objective with No. 4 compensating ocular.

LIST OF ABBREVIATIONS.

ann.	Ring of protoplasmic granules.
ax.	Cylindrical axis of the "nipple" in Trichonympha.
cil.	Cilia.
csp.	Tooth-like processes of the inner surface of the outer layer of the "bell."
deu'mer.	Deutomerite.
fbr. lig.	Wood fibre.
fg.	Flagellum.
fis.	Fissure.
mu.	Muscle.
nl.	Nucleus.
nll.	Nucleolus.
pd.	Peduncle.
pil.	Cap.
pli.	Fold.
pr'mer.	Protomerite.
pr'pl.	Coarsely granular protoplasm of "bell."
pr'pl′.	Finely granular protoplasm, making up most of the contents of the "bell."
pr'pl. ax.	Protoplasm situated in longitudinal axis of the bell of Trichonympha, which is coarser and more deeply stained than the surrounding protoplasm.
spo.	Spores of a fungus.
st.′	Inner layer of "nipple" and "bell" of Trichonympha.
st.″	Middle layer of same.
st.‴	Outer layer of same.
st. ctx.	Cortical layer of granular protoplasm.
st. gran.	The granular protoplasmic layer separating the "bell" from the posterior part (body) of Trichonympha.
st. gran.′	Granular protoplasm marking the region of transition from the superficial (ectosarc) to central (entosarc) portion of the protoplasm in the posterior half ("body") of Trichonympha.
st. str.	Striated layer of the "bell" of Trichonympha.
tub.	Knob-like enlargement of the anterior end of the protoplasmic axis of the "nipple," Trichonympha. Also knob-like structure at the anterior extremity of Pyrsonympha.

PLATE 1.

All figures are of Trichonympha agilis.

Figs. 1, 2. Normal appearance of parasite when examined in diluted albumen. × 520.

Fig. 3. Appearance of anterior tip of Trichonympha viewed from in front.

Figs. 4–6. Animals in diluted milk, showing corpuscles seized upon by the long rigid cilia and dragged after the animal. × 520.

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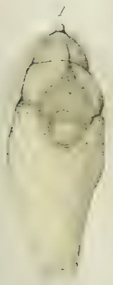

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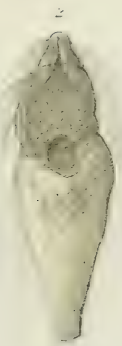

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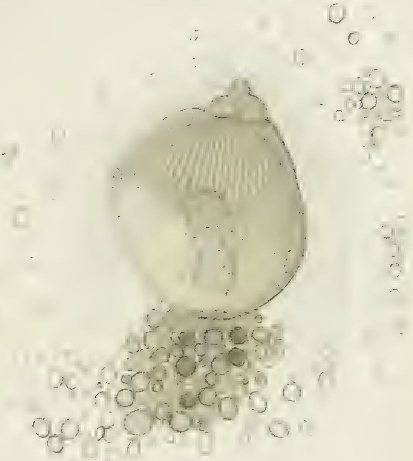

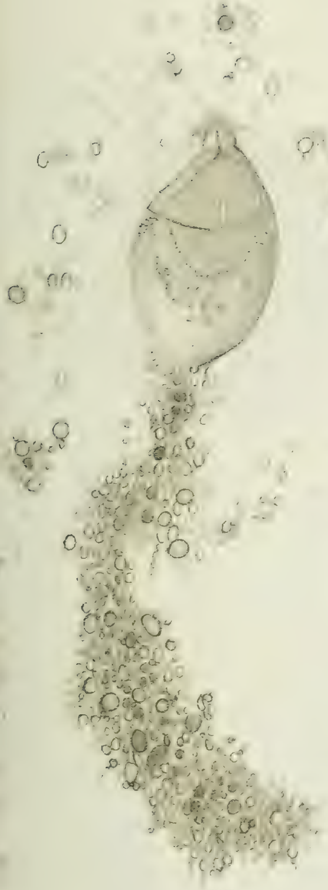

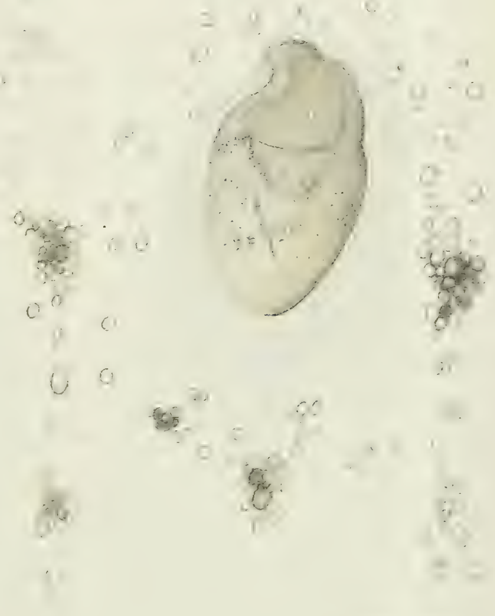

PLATE 2.

All figures are of Trichonympha agilis.

Fig. 7. Diagrammatic longitudinal section through the anterior portion of Trichonympha, imagined to be not thicker than one band of cilia.

Fig. 8. Same as Figure 7, but showing an additional layer (*st.''*) in the nipple-like anterior extremity.

Fig. 9. Cross section through posterior portion or "body," showing a fold in the body-wall, in which cilia have been engulfed.

Fig. 10. Section similar to that of Figure 9, except that particles of wood fibre are entangled with the cilia in the engulfed portion.

spo. Spores of Fungi eaten by the animal.

Fig. 11. Diagram of a portion of the surface of the anterior end, the "nipple," and part of the "bell."

Fig. 12. Diagram of side view of same region as that shown in Figure 11.

Fig. 13. Complete longitudinal section, showing a gathering of a clear protoplasmic substance about the nucleus; probably an early stage in the development of an immensely thickened nuclear membrane such as is shown in Figure 22.

Fig. 14. Cross section of posterior portion, showing a fold, as in Figures 9 and 10, the walls of which are beginning at *a* to disintegrate.

Fig. 15. Complete longitudinal section of an individual more shortened than that of Figure 13.

Fig. 16. Cross section in the region of the line 16–16, Figure 15.

Fig. 17. Diagrammatic cross section in the same region as Figure 16.

Fig. 18. Cross section of the nipple-like anterior extremity.

Fig. 19. The second section in a series of longitudinal sections. This is a portion of the bell, the outermost layer having been cut off with the first section from the middle of the figure, but remaining around the margin. In the centre is exposed the striated layer and the roots of the cilia arranged in quincunx.

Fig. 20. Diagram of the condition shown in Figure 19.

Fig. 21. Cross section in the region of the line 21–21, Figure 15, showing the radiating structure of the wall (*st. gran.*, Fig. 7) separating the anterior from the posterior half of the animal.

Fig. 22. Longitudinal section showing an immensely thickened nuclear membrane.

Fig. 23. Cross section in the region of the line 23–23, Figure 15.

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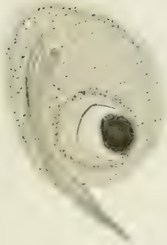

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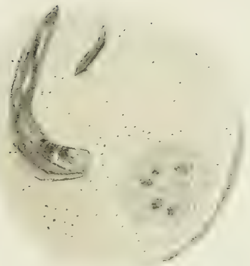

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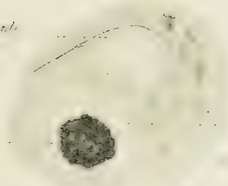

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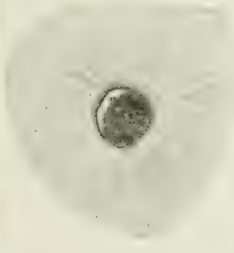

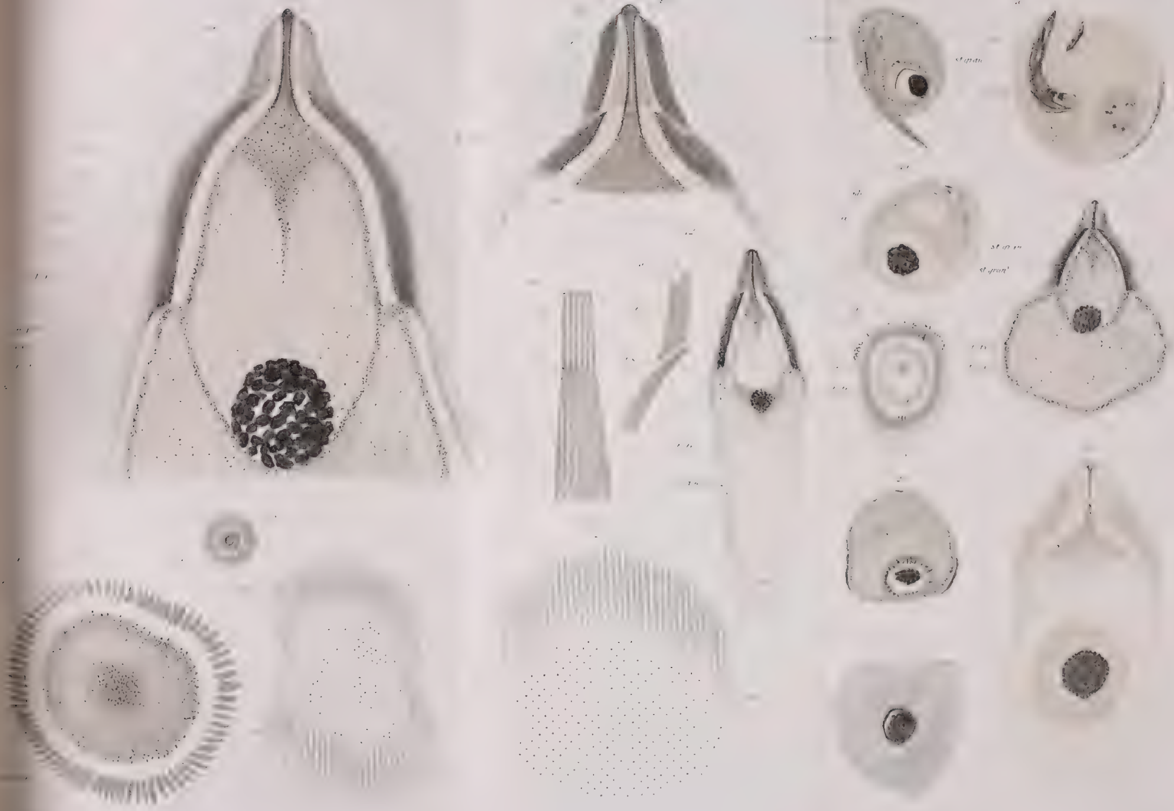
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PLATE 3.

Figs. 24–26. Trichonymphæ showing conditions which may be preparatory to longitudinal division. Compare text. × 520.

Fig. 27. A parasite supposed by Leidy to be a young stage of Trichonympha. × 520.

Fig. 28. Another similar individual with a peculiar swollen cap. × 520.

Fig. 29. An individual more highly magnified. × 1100.

Figs. 30–32. Young heretofore considered as immature Trychonymphæ, but which I believe to be a distinct species. × 520.

Fig. 33. Longitudinal section of a Pyrsonympha. × 400.

Fig. 34. A Pyrsonympha containing wood fibre, the flagellum protruding in a tail-like appendage from the posterior or unattached end. × 400.

Figs. 35, 36. The same kind of parasite as is shown in Figures 30–32.

Fig. 37. The same kind of parasite as those shown in Figures 30–32, 35, 36, but drawn from a living specimen. × 520.

Fig. 38. The same as Figure 37, but just after death in normal salt solution. × 520.

Fig. 39. The same kind of parasite as that shown in Figure 37. × 520.

Fig. 40. A Pyrsonympha apparently in the act of engulfing a particle of wood fibre. × 400.

Fig. 41. A Pyrsonympha with a peculiar flagellum. × 520.

Figs. 42–44. The same kind of parasite as that shown in Figure 39. × 520.

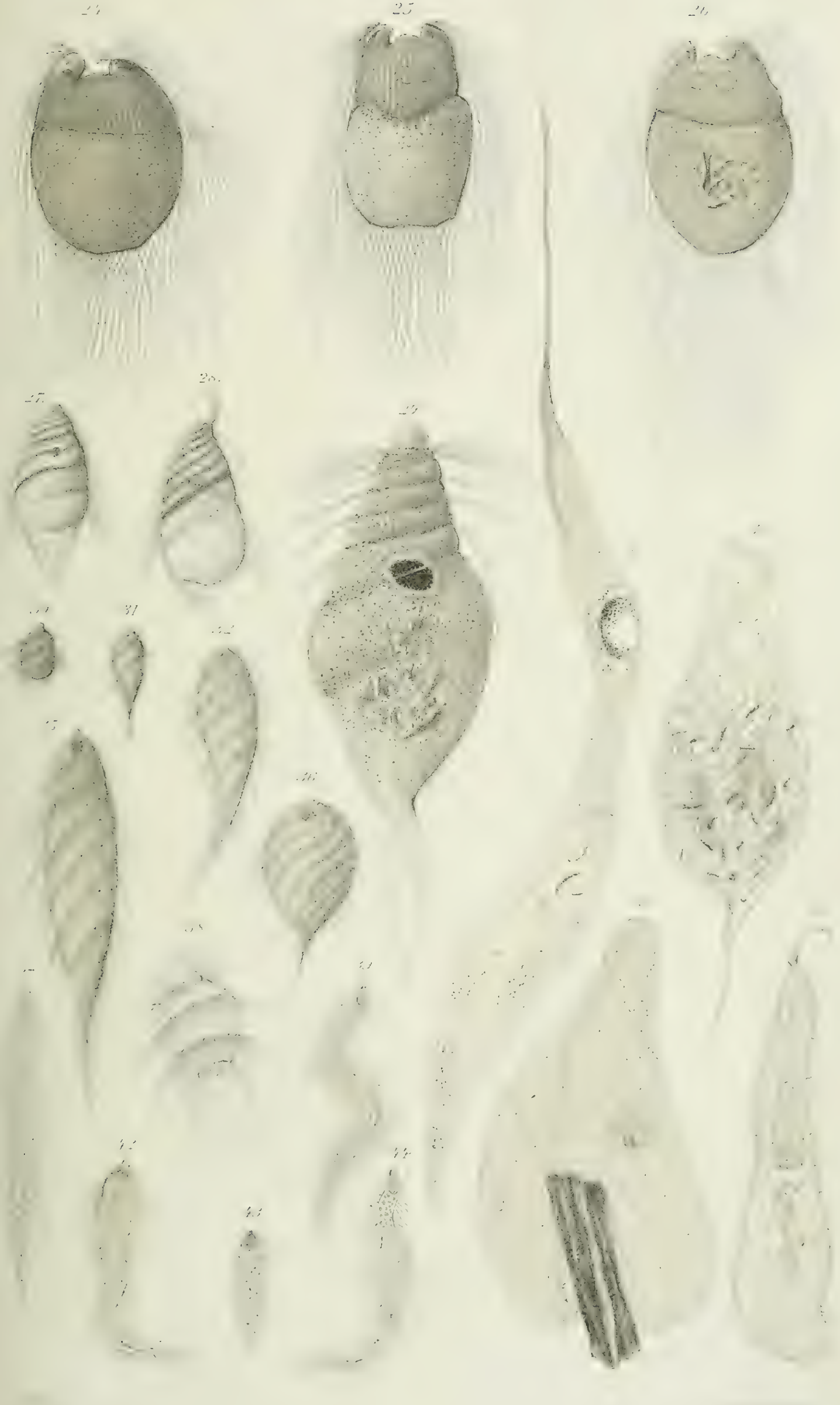
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PLATE 4.

All figures are of Pyrsonympha vertens.

Fig. 45. Parasites attached by peduncles to a bit of the intestine of the host. Drawn from living specimens. × 400.

Fig. 46. Optical section of anterior portion of a Pyrsonympha, showing the relation of the knob-like structure (*tub.*) to the flagellum on one side and the peduncle on the other. × 1100.

Fig. 47. Anterior portion of an individual, showing the nucleus and the superficial muscular cords. × 1100.

Figs. 48, 49. Nuclei in stages of division.

Fig. 50. A very much attenuated nucleus.

Fig. 51. Surface view of a Pyrsonympha. Between the spiral muscular cords are bands of granular protoplasm. The region at *a* is bare of all muscular cords. At the extreme posterior portion are several ring-like markings (*ann.*). × 400.

Fig. 52. Cross section through the animal in the region of the nucleus. × 1100.

Fig. 53. Optical longitudinal section of a Pyrsonympha with its nucleus in the posterior half of the body. × 520.

Fig. 54. Portion of the surface of a Pyrsonympha, greatly magnified, showing a finer and a coarser set of muscular cords. The cords of the finer set are surrounded by a clear homogeneous substance, while granular protoplasm surrounds those of the other set.

Fig. 55. Optical section of the Pyrsonympha represented in Figure 51. There are two nuclei flattened against each other. × 400.

P[illegible]R.-TRICHONYMPHA. PLATE 4

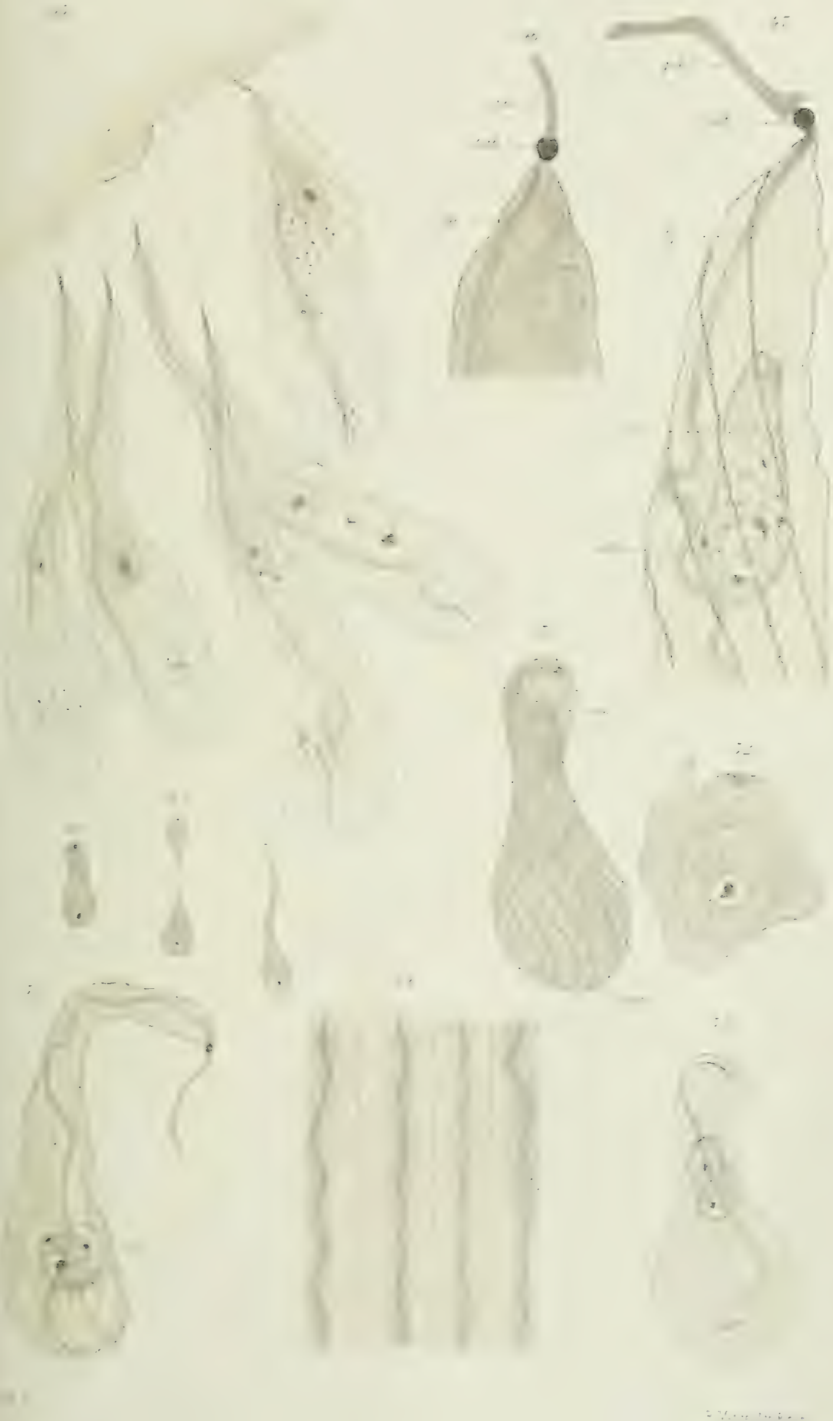


PLATE 5.

All figures are of Pyrsonympha vertens.

Fig. 56. Section of a portion of the intestine of a Termite, showing numerous young Pyrsonymphæ, the manner in which they attach themselves to the host, and the effect on the cells of the intestinal wall. × 1100.

a, *a*. Spaces due to shrinkage.

Fig. 57. Young Pyrsonympha without a flagellum. × 520.

Fig. 58. Young with a flagellum. × 520.

Figs. 59, 60, 65. Some of the shapes taken by a single living immature individual in the course of a few minutes.

Fig. 61. Young, showing that the flagellum takes the same direction as (is differentiated from ?) one of the superficial muscular cords. × 1100.

Fig. 62. Small Pyrsonympha, perhaps recently formed by division. × 520.

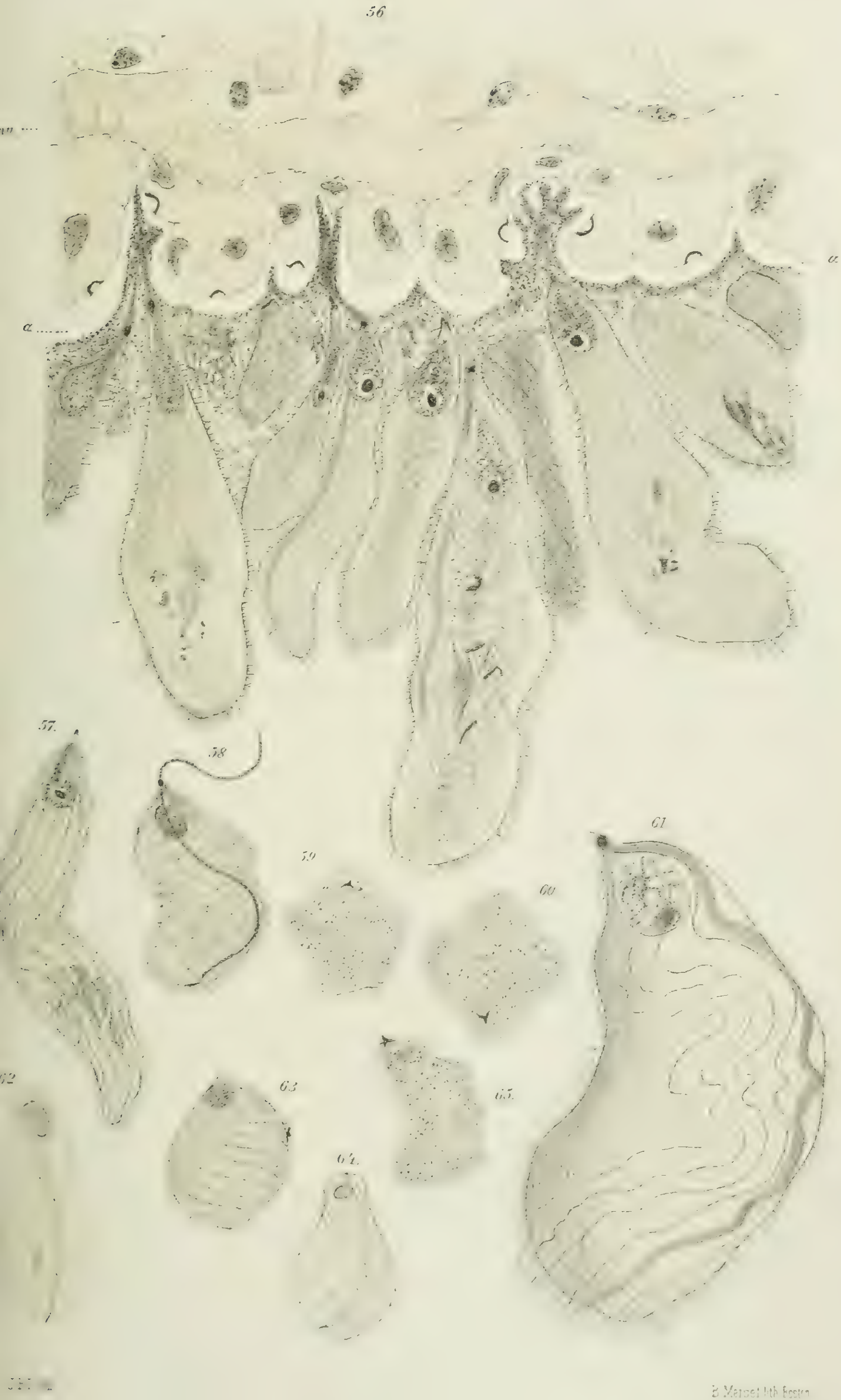
Fig. 63. Young Pyrsonympha without a flagellum. × 520.

Fig. 64. Small individual.

Fig. 65. Same individual as that shown in Figures 59 and 60.

PORTER.- TRICHONYMPHA.

PLATE 5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B. Meisel lith. Boston

PLATE 6.

Figs. 66–68. Common forms of Dinenympha. × 1100.

Figs. 69, 70. Surface views of the upper and lower sides of the same Dinenympha. × 1120.

Figs. 71, 72. Similar views of another individual. × 1120.

Figs. 73–76. Views of a Gregarine found as an intestinal parasite in Termes in company with Trichonymphidae.

Fig. 73. Normal appearance of a living Gregarine. × 520.

Fig. 74. A gregarine filled with sporocysts. × 430.

Fig. 75. Longitudinal section of a portion of the small intestine of a Termite, showing numerous Gregarines. × 150.

Fig. 76. Longitudinal section of a Gregarine. × 1100.

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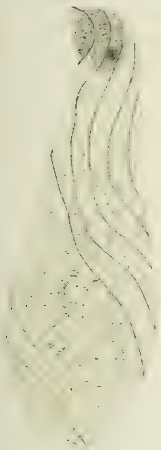

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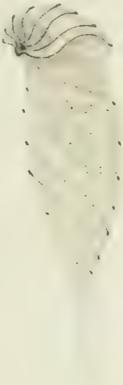

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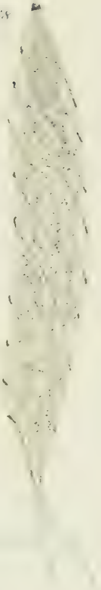

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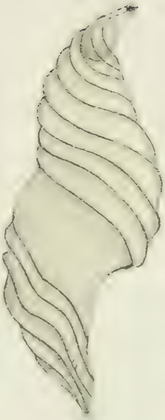

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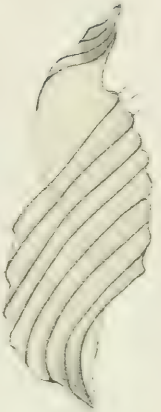

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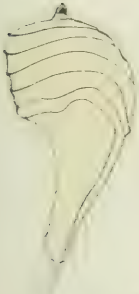

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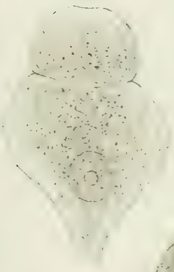

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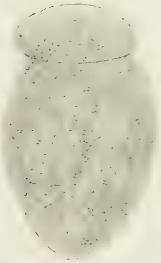

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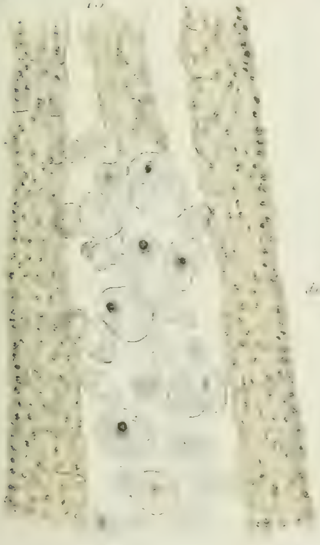

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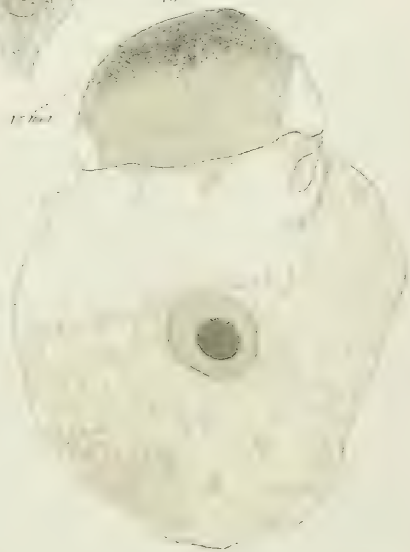

E. Meisel lith. Boston

No. 4. — *Variations in the Brachial and Lumbo-Sacral Plexi of Necturus maculosus Rafinesque.*[1] By F. C. WAITE.

VARIATIONS in the position of the pelvic girdle in Vertebrates, especially in Amphibia, have already been noticed by several authors; Adolphi, Bourne, Case, Howes, G. H. Parker, and others. These variations, which obviously involve an inconstancy in the number of presacral vertebræ, are as a rule symmetrical, the entire girdle being one segment caudad — more rarely cephalad — to the usual position; but infrequent instances are found in which the right and left constituents of the girdle have unsymmetrical positions.

Closely associated with the pelvic girdle is the lumbo-sacral plexus, and the problem which suggests itself in this connection is to determine whether, with the variations known to occur in the skeletal structures of the girdle, there are correlated variations in the lumbo-sacral plexus.

If, as some morphologists believe, a difference in the position of the sacrum is the result of increase in the number of vertebræ by splitting of one or more presacral vertebræ, or decrease through fusion, then such phenomena must take place in one or the other, or both, of two regions, either anterior to the most posterior nerve of the brachial plexus, or between that point and the lumbo-sacral plexus.

To obtain evidence upon these alternatives, I dissected out the brachial plexus, in addition to the lumbo-sacral, in all the specimens which I have studied. As this plexus involves less variation than does the lumbo-sacral, I shall discuss it first.

In naming the spinal nerves, I have adopted the plan of calling that nerve which emerges between the cranium and first vertebra the first nerve,[2] succeeding nerves being consecutively numbered.

So far as I have noticed, there is little variation among either the sympathetic or dorsal branches of the spinal nerves. Since only the ventral branches enter the plexi, I shall, for the sake of brevity, designate the ventral branch of the first spinal nerve as nerve I, the ventral branch of the second as nerve II, etc.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXXV.

[2] In the Anura, where there is no spinal nerve emerging anterior to the atlas, the so called first spinal nerve emerges between the first and second vertebræ, and is homologous to the second nerve of Urodela.

It has seemed necessary in comparing plexi to indicate in some way the relative value of the nerves entering them. I have therefore recorded their approximate diameters, which I shall designate as their strength, — a rough method, but accurate enough for the present purpose.

The material which I studied consisted of thirty specimens of the large perennibranch salamander of the Middle United States, — Necturus maculosus Rafinesque. These specimens were obtained from the Great Lake Region, in the main from a single locality (near Sandusky, Ohio) on the south shore of Lake Erie.

Unfortunately, I neglected to note the sex of each individual. The importance of this did not occur to me until the urogenital system had been removed, and dissection had gone so far as to prevent the determination of the sex. The greater number (more than two thirds) were males, but which ones I am unable to say.

The work represented by this paper was done at the suggestion, and under the direction, of Dr. G. H. Parker, to whom I am indebted for assistance and advice during its progress.

THE BRACHIAL PLEXUS.

The brachial plexus (Plate **1**, Fig. 1) is formed from nerves I to V inclusive. In no case have I found indications that nerve VI contributed to it.

The greater strength of the plexus lies posterior to the pectoral girdle. Its major part is compacted into a large trunk, the brachial nerve *(br.)*, which, after sending branches to the shoulder muscles, divides to supply the various muscles of the fore leg. But nerve distribution does not concern us here. It is my purpose to determine if, in the number and strength of the nerves which enter the brachial plexus, there be any variation which may be correlated with the variations in the sacral region.

If, when the sacral rib is on the 19th vertebra, — the more usual position, — we find the brachial plexus constant in position, and if, when the sacral rib is on the 20th vertebra, — a common variation, — we find a backward displacement of the brachial plexus to the extent of one segment, it would be fair to infer that the seat of variation is in the pre-brachial region.

Nerve I (Fig. 1) is slender, and does not contribute to the innervation of the appendage, but is distributed to the inner wall of the girdle. It often lies close to nerve II, and may (six cases in thirty) anastomose with it.

Nerve II is also slender, and is distributed to the same region as is I. It seems questionable if I and II can be properly considered parts of the plexus. In strength they approximate the ordinary post-brachial spinal nerves (VI to XV). In some cases branches of II run in close relation to the supracoracoid (*su'crac.*) branch of III, and may (four cases in thirty) pass out through the coracoid foramen with the supracoracoid. In no case have I found any anastomosis between branches of II and III, as implied by Hoffman ('74, p. 229) in his account of Necturus (Menobranchus); and from my specimens of Necturus I can assert that this is certainly not a constant relation, if indeed it occur at all.

Nerve III usually divides into three branches, of which the small anterior one is distributed to the thoracic wall, the middle one forms the supracoracoid nerve (*su'crac.*), while the larger posterior branch enters the main trunk of the plexus.

Nerve IV is usually the strongest trunk of the plexus. It passes directly to its exit posterior to the scapula, close to the margin of the glenoid cavity, giving off in its course a single small branch, which is distributed anteriorly on the thoracic wall. Before reaching the border of the scapula this nerve usually divides into two main branches, which pass side by side to the musculature of the anterior appendage.

Nerve V is the most posterior nerve to enter the plexus, its anterior branch joining nerve IV just before this reaches the scapula, while the small median and the posterior branches are distributed to the body wall, posterior to the girdle.

There were no variations of note in the *topography* of the plexi in the thirty animals examined, except in one case of slight want of symmetry in the point of junction of V with IV, but this occurred in a specimen which was normal in its sacral structures. Some variation occurs in the *relative strengths* of the nerves; for while IV is usually the strongest, it may be equalled by III, as was seen in six cases, of which four were with the sacrum in a normal position (19th vertebra), one with the sacrum on the 20th vertebra, and one with an unsymmetrical sacrum (Plate **2**, Fig. 5). Again, nerves III and V are usually of about equal strength, but III may be much (six to eight times) stronger than V, or more rarely may be weaker.

These conditions show a tendency toward variation in the location of the "strength-centre"[1] of the plexus, such variation usually resulting in displacement anteriorly; but this is not correlated with the variations in the position of the pelvic girdle, — indeed most such cases were found in specimens in which the pelvic girdle was normally placed, — nor have I found any correlation between the displacement of the strength-centre in the brachial and lumbo-sacral plexi respectively. This is not in accord with the conclusions of Adolphi ('96, p. 118), who says for Anura " . . . die beiden Extremitätenplexus, der Plexus sacralis und der Plexus brachialis, ihren Schwerpunkt in der gleichen Richtung verlegen . . ." Such a condition indicates that the variations in the brachial plexus are independent of variation in the position of the pelvic girdle; and since there is no posterior displacement of the brachial plexus, nor any change of topography in cases where the pelvic girdle is placed on the 20th vertebra, we have evidence that *there has been no interpolation of vertebræ in the part of the column anterior to the posterior limit of the brachial plexus.*

THE LUMBO-SACRAL PLEXUS.

The variations in the lumbo-sacral plexus are most conveniently grouped under three heads, viz.: A, those in which the girdle is attached to the 19th vertebra; B, those with the girdle carried by the 20th vertebra; and C, those in which the constituents of the girdle have an unsymmetrical position (see the Table, page 81).

Group A is represented by twenty specimens. The nerves here forming the plexus (Plate **1**, Figs. 2, 3) are XVIII to XXI inclusive, neither XVII nor XXII in any case entering it. The plexus is distributed by three trunks. The anterior is N. ileohypogastricus (*il-h'ga.*), which is the anterior branch of nerve XIX, and extends cephalad on the inner body-wall; its strength and relation to other nervous parts seem uniform. The middle trunk (*cru.*) is N. cruralis (obturator), which passes out between the ilium and pubis, to be distributed to the anterior part of the thigh. The posterior is N. ischiadicus (*isch.*), which is the main trunk, and is distributed to the posterior part of the thigh and to the leg.

We may distinguish in the topography of the plexus two types, based on differences in the source of the branches which go to form N. cruralis and N. ischiadicus; these I shall designate as α type and β type.

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[1] The term "strength-centre" has been adopted to designate that point in the plexus which is central with regard to the combined "strengths" of the component nerves. We may thus conceive the whole "strength" of the plexus as concentrated at this point, the "strength-centre."

In the α type (Plate **1**, Fig. 2) N. cruralis (*cru.*) is formed from the union of the posterior branch of XIX with a small anterior branch of XX, while N. ischiadicus (*isch.*) is formed by union of the remaining part (posterior branch) of XX with the anterior branch of XXI.

In the β type (Plate **1**, Fig. 3) N. cruralis (*cru.*) is the middle branch of XIX, which may (three cases out of ten) receive a delicate branch from XVIII; while N. ischiadicus (*isch.*) is formed by union of the small posterior branch of XIX, all of XX, and the anterior branch of XXI.

It will be noticed that the α type (Fig. 2) presents, as compared with the β type, a tendency to a forward migration of the plexus as a whole, indicated by part of nerve XX trending forward into the next segment to enter N. cruralis; on the other hand, the β type (Fig. 3) shows a backward tendency, since nerve XIX sends a branch into the next posterior segment to enter N. ischiadicus, and also nerve XVIII occasionally enters into N. cruralis.

The successive spinal nerves in the region of the plexus may now be considered individually.

Nerve XVIII makes only a small and inconstant contribution to the plexus, since in three cases only, — all in the β type, — it gives a delicate branch to N. cruralis. Its strength is nearly constant, and is about the same as that of the ordinary spinal nerves anterior to it. This nerve may therefore be considered as a nearly typical spinal nerve.

Nerve XIX presents much variation in its strength relative to the other nerves of the plexus. It may equal XX, — six cases in twenty, — or it may have only $\frac{1}{4}$ the strength of that nerve. Its average strength as compared with nerve XX (the main nerve of the plexus) is between $\frac{1}{2}$ and $\frac{2}{3}$, and this is the relation usually found. Besides the ileo-hypogastric branch, which is constant, this nerve possesses one (type α, Fig. 2) or two (type β, Fig. 3) branches. In the β type the middle (cruralis) and posterior branches show considerable variation in strength in relation to each other.

Nerve XX is the chief nerve of the plexus. Its strength is usually about eight times that of an ordinary spinal nerve. In the α type, it gives off a branch anteriorly, which joins the posterior branch of nerve XIX, these together forming N. cruralis. This anterior branch is always much weaker than the remaining (posterior) one, which forms the major part of N. ischiadicus. In the β type the entire nerve becomes a part of N. ischiadicus.

Nerve XXI has a uniform relation to the plexus in the two types. Its stronger anterior branch enters N. ischiadicus, while the weaker posterior branch is distributed to the wall of the pelvic cavity. The strength of the whole nerve before branching varies from $\frac{1}{4}$ to $\frac{2}{3}$ that of nerve xx, the average being between $\frac{1}{3}$ and $\frac{1}{2}$; i. e. it is usually weaker than nerve xix, but may (four cases in twenty) equal that nerve in strength.

To gain evidence on the relation of the plexus to the skeleton, I have in each specimen determined the position of the first vertebra which bears a hæmal arch, for this is often assumed as a fixed point in discussing variations in the vertebral column. By reference to the Table on page 81, (see also Parker, '96, p. 712, and Bumpus, '97, p. 457,) it is seen that the position of the first hæmal arch is variable; but, as the following tabulations show, there is no correlation between these variations, and those of the "strength-centre" of the plexus as represented by the α and β types.

α type, with first hæmal arch on vertebra $22 = 4$ cases.
α " " " " " $23 = 6$ "
β " " " " " $22 = 6$ "
β " " " " " $23 = 4$ "

Group B includes the individuals having the sacrum borne on the 20th vertebra, and of these there were seven specimens. The nerves involved in the plexus (Plate **1**, Fig. 4) are xix to xxii inclusive. Nerve xviii in no case entered the plexus. In three cases a delicate branch from xix was contributed to the formation of N. cruralis. Nerve xix occupies the same relative position as did nerve xviii in group A, but shows more of a tendency to enter the plexus (three cases in seven, as against three cases in twenty in group A) than did the element in the same position in group A. Moreover, it is distinctly (a half) stronger than are the ordinary spinal nerves. For these reasons it must be considered as belonging to the plexus.

Nerve xx corresponds in position and distribution to xix in group A. In every case it branches into three parts, the anterior forming N. ileohypogastricus, the middle N. cruralis, and the posterior entering N. ischiadicus; i. e. the β type of group A only is represented, but with the modification that at first sight the whole plexus is *apparently* one segment posterior to the position in the β type specimens of group A.

The whole of nerve xxi in each case enters into the formation of N. ischiadicus, for it sends no important branches cephalad or caudad. Its strength averages six times that of an ordinary spinal nerve, i. e. it is a fourth weaker than the nerve (xx) occupying the corresponding position in group A. Its average strength is about $1\frac{1}{4}$ times that of the next anterior nerve, while in group A the ratio is $1\frac{2}{3}$ to 1.

Nerve XXII has here topographically the same relations as nerve XXI in group A, but its strength relative to the rest of the plexus is much less, and in two cases (in seven) *it fails to send a branch into the plexus.* The position of the first hæmal arch is in every case on the 23d vertebra.

At first sight the whole plexus in group B seems to have moved with the girdle one segment caudad as contrasted with the position in group A, a condition which might be explained by the interpolation of a presacral segment; but for several reasons I do not believe such an explanation to be sufficient. If a presacral segment had been interpolated, thus entailing a change in position to the extent of an entire segment, we should expect still to see variations in the position of the first hæmal arch. In one half the cases in group A (see Table, p. 81) the first hæmal arch was on vertebra 23, *three* segments posterior to the main nerve of the plexus. Hence in group B, if the interpolation hypothesis be true, the hæmal arch ought to occur, at least occasionally, in the same relative position, i. e. on the 24th vertebra, instead of maintaining as it does a constant position on vertebra 23, only *two* segments posterior to the main nerve (XXI) of the plexus. The specimens examined by Parker ('96, p. 712) show the same result, i. e. a constancy of position of the first hæmal arch on the 23d vertebra in all specimens bearing the girdle on the 20th vertebra. Bumpus ('97, p. 473), however, among thirty-five specimens having this position of the girdle finds three (9%) in which the first hæmal arch is on vertebra 24. This shows that such a position, though possible, is rare.

Again, we should not expect the tendency of the last trunk nerve (XVIII in group A, XIX in group B) to enter the plexus to be so much greater in group B (43%) than in group A (15%), nor should we expect to find its strength in group B distinctly exceeding that of the ordinary spinal nerves, as it does, since there is no indication of such an excess in group A.

If interpolation has occurred, nerve XXII should show about the same average relative strength as the element (XXI) corresponding to it in group A. This is not found to be so, for XXII in group B is relatively and absolutely *much* weaker than XXI in group A, and by completely failing in two cases (28%) to enter the plexus shows an inconstancy not seen in the corresponding nerve (XXI) in group A. This leads to the conclusion that in group B this most posterior nerve (XXII) is not an essential element of the plexus.

Nerves XX and XXI in group B correspond, in position relative to the sacrum, to nerves XIX and XX in group A (cf. Fig. 4 with Figs. 2 and 3). In group A the main nerve (XX) has eight times the strength of an ordinary spinal nerve. In group B the main nerve (XXI) is but six times as strong as this unit. In group A nerve XIX has an average strength $\frac{1}{2}$ to $\frac{2}{3}$ that of nerve XX; though in some cases (30%) their strengths are equal, in others XIX may have only $\frac{1}{4}$ the strength of XX. In group B, on the other hand, in two cases only is XX weaker than XXI; in three cases their strength is equal, and in two cases XX is the *stronger*, i. e. in 70% of the cases XX equals or is stronger than XXI. The average strength of XX as compared with XXI is as 1.1 to 1 in group B, whereas in group A the ratio between the corresponding elements is about 0.6 to 1. This shows that in group B the main nerve (XXI) tends to be weaker, and the one next anterior to it (XX) to be stronger than the corresponding nerves (XX and XIX) in group A. This, together with the weakness and inconstancy of XXII in group B, and the greater strength of XIX with its increased tendency in this group to enter the plexus, is evidence that in group B the *strength-centre of the plexus has not travelled caudad through an entire segment* as compared with group A, *but holds a position intermediate* between such an one and that of group A.

If we adopt as an explanation of the above facts and conclusion the interpolation of a presacral segment, we shall have to supplement such an explanation by assuming a subsequent movement cephalad of the plexus as a whole, to account for the ascertained intermediate position of the strength-centre of the plexus.

From the evidence of the hæmal arch, and of the topography (β type) of the plexus, — which I shall immediately discuss, — it seems more reasonable to consider this intermediate position of the plexus the result of what may be called the migration caudad of the locus of the strength-centre. The correlation of the position of this locus with that of the girdle I shall discuss further on.

There is in group B a persistence of the β type of topography. This at first may seem to contradict the conclusion that we have an intermediate position of the locus of the strength-centre, for with an intermediate position of the plexus arising from migration caudad we should expect traces of reversion toward the more anterior position, such as is indicated by the tendency cephalad in the α type. However, there are reasons for expecting the β type here. (1) In such posterior migration as is shown in group B, there must also be a tendency — whatever has been the stimulus to cause the migration of the locus of the whole plexus — for a movement caudad among the parts of the plexus, since the movement of the entire plexus is but the summation of the movements of its elements, the individual nerves. (2) Nerve XXII is so inconstant and contributes so feebly to N. ischiadicus, that, in compensation for this deficiency, all of XXI is taken up to form N. ischiadicus, and thus it can contribute nothing to N. cruralis. Again, I have shown that, in group B, XXI is relatively weaker, and XX relatively stronger than the corresponding elements of the plexus in group A. Hence a contribution from XX to N. ischiadicus (in group B) serves to make up the deficiency arising from the inconstancy and stronger posterior tendency of XXII (cf. Fig. 4). (3) It is to be noticed that in group A (Figs. 2 and 3), XXI *always* entered N. ischiadicus and that nerve *only*, while XX was (see Table) in many cases (α type) divided between N. ischiadicus and N. cruralis. This gives to XX the definite relation of a component part to N. cruralis in group A, a relation which might be expected to be retained after migration, i. e. in group B. But in group A XXI in no case had any relation to N. cruralis. It is therefore less probable that in the new condition XXI should form a new connection entering N. cruralis, than that it should give its entire strength to N. ischiadicus, as it does, with which it had the definite relation of a component part in the old condition. The general backward movement of the parts of the plexus, and the former (α type of group A) branched condition of XX, may account for the fact that this nerve sends a branch to N. ischiadicus in this post-migration condition.

These considerations lead me to believe that the β type is the only condition to be expected in group B, if the plexus has reached its position there by means of migration of the locus of its strength-centre. If however, interpolation of a presacral segment has occurred, we should expect to find about the same variations in type of topography in group B as in group A. These do not occur, therefore the persistence of the β type of topography in group B; the inconstancy of nerve XXII, and the added activity of XIX in their contributions to the plexus; together with the slight variation in the position of the first hæmal arch shown in this group; — all combine as evidence against the theory that the position of the pelvic girdle in group B is the result of interpolation of a presacral segment.

Group C includes three individuals (10% of the total number examined), in which the attachment of the girdle is unsymmetrical.

Of these one (Plate **2**, Fig. 5) bore the right sacral rib on the 19th vertebra, the left on the 20th, while the first hæmal arch was on the

23d vertebra. The topography of the plexus is of the α type. There is no asymmetry in its distribution to the appendages, although the plexus of the left side must as a whole trend further caudad in order to reach the foramina of exit. On the left side the backward trend of XIX exposes a longer antero-posterior area of the body wall to which XVIII is distributed than is exposed on the right side. In accordance with this, nerve XVIII of the left side is slightly stronger than its companion of the right side. Also nerves XIX and XX of the right side are somewhat stronger than their mates of the left side; i. e. the strength-centres of the two sides are to a slight extent unsymmetrically placed, but this by no means equals the extent of an entire segment.

To which group, A or B, is this specimen more closely related? As in both these groups the first hæmal arch may occur (see Table) on the same vertebra as in the specimen under consideration, this criterion is of no value in determining the affinity of the specimen. But the fact that the plexus of this specimen is of the α type indicates that it falls under group A, to which this type is restricted (see Table). A glance at Figure 5 shows that the main nerve of the plexus is XX, and that XXII fails to enter the plexus, both conditions typical of group A. Hence I consider this specimen to represent an individual like those of group A, in which, however, the sacral rib of the left side is displaced one segment caudad. There is not a corresponding displacement through one segment of the plexus of the left side, but only a *slight* displacement of the strength-centre caudad.

The two other unsymmetrical specimens (Plate **2**, Fig. 6) have in each case the right sacral rib on the 18th vertebra, the left upon the 19th. In both cases the first hæmal arch is on the 22d vertebra. The plexus is of the β type, but with the modifications that in both cases the posterior branch of nerve XVIII enters strongly into the plexus, and further in both cases nerve XXI does not enter the plexus, but remains a weak nerve distributed to the wall of the pelvic cavity. The plexus is consequently formed of nerves XVIII, XIX, and XX. Nerve XVIII is stronger than usual, XIX equals the strength of XX, and, as noted, XXI is very weak, being no stronger than an ordinary spinal nerve, all of which shows a displacement of the strength-centre cephalad. I can detect no marked want of symmetry in the locus of the strength-centre of the two sides, but if there be any, indications are that it is toward a yet further displacement cephalad of the plexus of the right side.

The position of the hæmal arch on vertebra 22 and that of the sacral ribs remove these two specimens from any relationship to group B, and I therefore conclude that they represent individuals like those of group A, in which the right sacral rib has been displaced cephalad through one complete segment. Superimposed upon this is a displacement cephalad of the strength-centre of the plexus through the extent of part of a segment only, as is clearly indicated by failure of xxi to enter the plexus, and the increased strength of xviii. These conditions together represent a state intermediate between that of individuals bearing the girdle symmetrically on the 19th vertebra, and a hypothetical group in which the girdle would be carried symmetrically on the 18th vertebra, and probably with the first hæmal arch on the 21st vertebra part of the time at least. Such a variation has not been described in Necturus, so far as I know, but I think it likely to occur, although the prevailing tendency in abnormal position of the girdle is toward displacement caudad. Indeed, Davidoff ('84, p. 412) has found such symmetrical displacement cephalad in Salamandra maculosa.

Of the 157 specimens of Necturus recorded by Parker ('96), Bumpus ('97), and myself, thirteen (8 %) are found to have unsymmetrical sacra. Of these thirteen, nine have the sacral rib of the left side further cephalad, four that of the right side. It is thus seen that unsymmetrical sacra are not very rare, and further that either side may be in advance. Of these four specimens with the right side in advance, three, one recorded by Bumpus ('97, p. 466) and two by myself, invade the territory of the 18th segment, and these three are the only cases out of the 157 in which that segment is invaded.

By way of summing up the statistics of certain of the conditions described, the following table of the thirty specimens which I have dissected is inserted: —

TABLE.

Vertebra which carries Sacrum.	Number of Specimens.	α Type.	β Type.	First Hæmal Arch on	
				Vertebra 22.	Vertebra 23.
19	20	10	10	10	10
20	7	0	7	0	7
19 (rt) and 20 (lft.)	1	1	0	0	1
18 (rt.) and 19 (lft.)	2	0	2	2	0

An interesting skeletal variation in one of the specimens of group C just described is the occurrence on the left side of the 19th vertebra of a bifurcate transverse process and a partially double sacral rib (Plate **2**, Fig. 7). The two sacral ribs are not distinct throughout their course, but articulate independently with the transverse processes, and normally with the ilium. This condition is parallel with the occurrence of bifurcated transverse processes on the vertebræ of Rana, as recorded by Bourne ('84, p. 87).

There has lately come into my possession a skeleton of this species, the soft parts of which had already been to a considerable extent removed. This skeleton shows (Plate **2**, Fig. 8) a single sacral rib on the left side borne on the 19th vertebra, while on the right side are *two* sacral ribs borne one each on the 19th and 20th vertebræ. These ribs are both well formed, but the posterior one is much the shorter, and from comparison with the other side, is evidently the supernumerary rib. Each articulates independently with the head of the ilium, and all the joints work easily. The transverse process on the left side of the 20th vertebra shows no trace of a rib or articulation, and as it was well covered with the musculature, which had not been disturbed when I received it, I am certain that none existed there. The condition of the specimen when received was such as not to allow determination of the nerve relations.

Theoretic Considerations.

The variations which have been described in the preceding pages involve at least two questions: (1) Does the abnormal position of the girdle arise by intercalation or excalation of presacral segments, by slipping of the girdle upon the column cephalad or caudad, or by some other means? (2) Is there any correlation between the variations of the plexus and those of the girdle, and if so, of what sort is it?

The first of these questions is far reaching, and this paper does not aim at an exhaustive discussion of it. It is commonly held that nerves are less subject to variation than either muscles or skeletal parts, and thus serve as a surer basis for homology; yet this basis is in a degree unstable, for there are certainly considerable variations amongst nerves, as I have shown, for instance, in the lumbo-sacral plexus.

The evidence for intercalation or excalation as an explanation of the changes in the presacral length of the column is of a diversified nature, and the opinions concerning such a process may be roughly grouped in two categories: first, that the change in number of segments is due to an initial variation in the serial number and position of centres of metamerism, — a doctrine formulated by Bateson ('92, p. 111); and, secondly, that such change arises from fusion of two or more adjacent somites, or from the splitting of one or more somites somewhere in the presacral region. The first of these two views is the more acceptable as a morphological process, as it preserves the integrity of the metameres and makes the process a general one affecting the animal as a whole, rather than localizing the activity within narrow limits, but the evidence in its favor is mostly *a priori*.

Rosenberg ('76, p. 104) was one of the first to advance such a view, but he went further than is implied in the above statement, and held that this process is an actively phylogenetic one, and that in the vertebrate series its operation results in a constant shortening of the vertebral column. This shortening is greatly emphasized in some orders, e. g. Anura, whereas such conditions as occur in Ophidia must, on the contrary, be considered reversionary.

According to his view, in the early ontogeny there is represented the primitive condition with a very large number of separate prosegments, but in course of development of the individual these are reduced to the number set by heredity. We may infer variation in the final number of segments to be the result of inaccuracy of response to the hereditary stimulus. As noticed by many writers upon this subject, the great majority of such variations are toward an increase in the number of segments, and according to this view such cases must be interpreted as atavistic. It would seem that Rosenberg's view is insufficient, or at least if there be such a general tendency, it is exerted, not in a single unilateral series, but in a branching series of phylogenetic relationships.

In such cases of variation between two individuals either of the same or of different species, no one centre of the final series of metameres in the normal can be directly homologous with any one centre in the variant; i. e. the number of segments arising in the variant differs from that arising in the normal, and each segment occupies a new position different from that in the normal.

Most of the evidence from recorded skeletal abnormalities better fits the second category stated. Baur ('91, p. 335) claims intercalation of vertebræ as an actual ontogenetic process. This is based upon the evidence afforded by certain complexes of vertebræ which show incomplete fission on one side of the median plane, with a normal condition on the other side, these having been recorded in some Ophidia by Albrecht, Owen, and Baur himself. Other cases of vertebral "masses" have been described by Bourne ('84, p. 86), Benham ('94, p. 477), Adolphi ('96, p. 133), and others. But such masses may, in my opinion, better be interpreted as ankylosis, symmetrical if the line of fusion be transverse to the axis of the column, or unsymmetrical if the line of fusion has been oblique. This is borne out by the fact that near, though not necessarily contiguous to such an unsymmetrical mass, there is usually found a complementary mass (see Benham, '94, pp. 477, 478); i. e. if by oblique fusion we have a mass containing one right half-vertebra and two left halves, we shall find near by another mass representing one left half-vertebra, and two right halves. The vertebræ lying between these two masses will be morphologically oblique, their two halves in each case belonging to different somites, although the adjustment of growth may have brought these to an apparently normal position, with transverse axis at right angles to the main axis of the column. That the right and left halves of a vertebra may slide upon each other, is held by Adolphi ('96, p. 136) to be confirmed by embryological evidence. Such unsymmetrical masses have not been accompanied by correlative asymmetry in musculature and nerves where the soft parts have been described.

Symmetrical fusion of vertebræ has been described by Howes ('93, p. 295), Adolphi ('95, p. 466, and '96, p. 122), and others. An actual increase in number of vertebræ, and also an indicated increase by grooving and partial splitting of vertebræ, and by bifurcation of transverse processes, have been noticed by Bourne ('84, p. 87), Benham ('94, p. 478), and others. The cases of actual increase described were in Anura, and resulted from separation of the anterior portion of the urostyle as a supernumerary vertebra. Adolphi ('95 and '96) has recorded forty-three cases of vertebral fusion in Bufo, Pelobates, and Rana, and has determined the nerve relations. He finds that in such cases of fusion the spinal nerves are not suppressed, but emerge through foramina in the fused mass; they are, however, liable to be weaker than normal.

Such supposed direct evidence of intercalation and excalation is capable of being interpreted as pathological, rather than as a disturbance tending primarily to alter the serial number of metameres, — especially since it is almost entirely confined to the skeleton, without involving musculature or nerves beyond the narrow limits necessitated by local accommodation to the distorted vertebræ. No evidence of the inheritance of such abnormalities has yet been offered. Such would be valuable as determining whether or not these variations show persistence. If so, it would indicate that they are sports; if not, the pathological interpretation would be strengthened.

I have shown that no intercalation or excalation is evident in the prebrachial region of Necturus, and since serial variation tends to be at one end of the series, it is more to be expected in the prebrachial region than in the postbrachial-presacral region. Addition or loss at the caudal end of the series may be disregarded, as this could not directly affect the number of presacral vertebræ, although it might be correlated with an abnormal position of the sacrum, both being an indication of general instability in the individual.

While the idea of variation in the number and position of centres of metamerism may be attractive on theoretic grounds, it has no observational evidence to support it, and, further, is insufficient to account for unsymmetrical sacra and supernumerary sacral ribs. On the other hand, intercalation or excalation has not been shown to exist as a morphological process, the supposed evidence for it being more naturally interpreted as due to pathological conditions. Since these two explanations seem improbable, we must look for some other cause of the variations of presacral distance which we find.

The common expression of sliding or shoving of the sacrum upon the column is open to criticism. It is contrary to ideas of metameric unity that the girdle should begin its development in one segment, and later in ontogeny migrate to the next. Bolk ('94, p. 267) has found in Homo during ontogeny an actual migration cephalad on the part of the Anlage of the pelvic girdle; but such migration is confined within narrow limits, not having extended over an entire segment, and thus the Anlage has not passed through a myotome. A slight migration of the musculature in relation to the skeleton is also known, but none of these slight changes are sufficient to account for sudden displacement of the girdle through an entire segment. Bumpus ('97, p. 464) has advanced a modification of this idea to account for the greater frequency of displacement caudad. Since the transverse processes to which the sacral ribs are attached lie nearer the caudad limit of the vertebra, he considers it "more probable that variations occurring in the course of ontogenetic development will fall on the side of nearer proximity," i. e. into the next segment caudad, and, having once invaded the territory of this new segment, the ribs will be adjusted to the proper position within that segment near the posterior limit. The individuality of segments in the skeleton is very sharp, and any explanation which involves a migration of an organ located entirely in one segment, so that it comes to lie wholly in another segment, assumes a process which is not only unproved, but seems to me highly improbable. Bumpus accounts for variation of the serial position of the sacrum by assuming that the appendage has a locus fixed at a point whose linear distance from the cranium is a definite and constant proportion of the entire length of the animal. The change in serial position of the girdle is then effected by compressing the presacral vertebræ, making each shorter and diminishing their combined length, thus bringing a vertebra caudad to the normal, opposite the stationary appendage locus. While such a view may be made to account also for asymmetrically placed sacra, it is difficult to see how it will adapt itself to the occurrence of supernumerary sacral ribs, and especially those asymmetrically placed (see Plate **2**, Fig. 8).

What seems most probable is that in different individuals the girdle may develop at primarily different distances (measured in segments) from the cranium. In Necturus we find a pair of sacral ribs on vertebra 19 (group A), or on 20 (group B). The explanation by intercalation implies that vertebra 20 in group B is the same vertebra as 19 in group A. That of slipping of the girdle — literally taken — implies that a girdle beginning to form in the 19th segment later (in ontogeny) is transferred to the 20th segment. Both explanations, as already stated, seem unsatisfactory. It is more logical to consider that the new position of the girdle is due to a stimulus to girdle formation having been applied at a *new* point, i. e. in a segment other than the normal, and hence that a sacral rib may arise in any one (or more, as shown in supernumerary ribs) of several points in this region. In Necturus these points are at least three, located in the 18th, 19th, and 20th segments.

Such a view explains the variation as to place of origin in different segments of sacra placed symmetrically, and also the condition of unsymmetrical sacra, such as have been described in group C, — since the stimulus to girdle formation is not single but paired, i. e. from the future appendages, and so need not necessarily be symmetrical; and above all it is sufficient to explain the occurrence of supernumerary sacral ribs. These latter may be on one side only (Plate **2**, Fig. 8, Howes, '86, p. 279, Lucas, '86, p. 562, and others); or a symmetrical pair of supernumerary ribs may appear (Case, '96, p. 232; Lucas, '86, p. 562).

From the foregoing discussion I conclude that *neither intercalation or excalation, nor slipping, are involved*, but that the abnormal position of the girdle represents development of a *new* girdle at a *new* point.

This new position is usually caudad to the normal, though in a few recorded cases in Urodela (Davidoff, '84, p. 412, and others) it is cephalad. Such general displacement caudad is capable of interpretation either as atavistic, or as indicating some force at work tending to lengthen the vertebral series.

It is noticeable that unsymmetrical relations of the appendages are more frequently recorded in Amphibia than in Reptilia, Aves, or Mammalia. This may possibly be due simply to the probably greater number of Amphibia examined. But assuming that this is not the case, it is not clear why such variation should exceed in this class. I offer, however, the suggestion that it may be due to the position of the embryo during development. In Amphibia the position is such that the embryo is curled within the egg membrane *laterally*, which would tend to shorten the concave side, and so might induce a displacement of the appendage of that side cephalad or caudad. In the other groups mentioned, the curling of the embryo is *dorso-ventrally*, and would give less tendency to unsymmetrical relations.

As to the second question involved, — Is there any correlation between the variations of the plexus and those of the girdle? — there is a wide difference of opinion, ranging from very close correlation, as maintained by Ruge ('93, p. 393), to no correlation, as believed by von Ihering ('78), who regards nerve and skeleton as independent in variation. Von Ihering holds that the plexus migrates as a whole independently of the girdle; if cephalad, then a presacral pair of spinal nerves drops out, if caudad, a pair is inserted, and if the migration be unsymmetrical, it involves loss or addition of a spinal nerve on one side only.

Such a scheme, by reason of its apparent artificiality, fails to appeal to me strongly, and no conditions found in Necturus warrant adoption of such a hypothesis.

The plexus is a combination of spinal nerves, the nature of whose topography is secondary. The point which needs emphasis in this connection is that the variation of the plexus is not a variation as a whole, but the summation of variations of its elements (individual spinal nerves). The variation in strength of these elements is probably a response to the influence from their end organs, — the muscles, — for there appears to be direct correlation between the size and activity of a muscle, and the strength of the nerve or nerves supplying it. Whether the muscles of a given metamere shall develop as limb muscles, i. e. muscles of increased size and activity, or into less extensive trunk musculature, depends upon whether or not in that region an appendage — the primary determinant of both plexus and girdle — is to arise. If appendicular musculature develop, the increased activity presumably induces stronger development of nerves in the segments involved, the matter of topography of plexus being secondary to the determination of the segmental position of the appendage.

That there is any direct correlation between skeletal and nervous tissues seems improbable, for there is no obvious reason why nerves should directly influence skeletal parts, nor is it probable that skeletal parts directly influence the position of nerves, since the vertebrate skeleton arises, both in phylogeny and in ontogeny, much later than the nervous system.

The view of the relations of nerve and skeletal parts, first hinted at by Fürbringer ('79), and more clearly formulated by Eisler ('92), seems much more reasonable than the idea of direct correlation. According to Eisler's conception, skeletal and nervous structures exhibit variations independently, but in parallel directions. The control of such parallelism rests with the musculature. The latter has very definite relations to the nerves on the one hand, and to the skeleton on the other. Bolk ('94) has shown that in Homo the position of the nerves depends upon the position of the muscle segment, which is differentiated earlier than the nerve, and it is also well known that the myomeres have very close relations to the vertebræ, so that in any given segment there is an interdependence among the three systems. Either nerve or vertebra may vary within certain limits, without necessarily affecting the other, but extensive variation of either would presumably influence the other through intermediation of the musculature.

From the nature of the case skeletal variations within narrow limits are less easily observable than nervous; but the examination of almost any series of vertebræ shows variation not only serially, but also on the right and left sides of the same vertebra. Such variations have been recorded by Paterson ('92, pp. 523, 524) from dissections of a large series (265) of human adults.

The conception of parallel variations of skeleton and nerve under control of the musculature is able to explain the fluctuations in position and strength of nerves belonging to any one segment involved in the plexus. It also offers an explanation of the inverse correlation of nerves of adjacent segments, seen in the weakening of the nerve of one segment, accompanied by a strengthening of that of the next segment; for since many muscles are innervated by two or more nerves from different segments, if one of these becomes weaker, the other becomes stronger to make up the deficiency. It should be remembered further that it has been shown that any one of several myotomes in this region is able to produce sacral ribs. In the greater number of cases the function of rib production by the myotome is expressed at a constant distance (measured in metameres) from the cranium, resulting in what we call the normal position; but as some tendency arises for the girdle to be abnormally placed, such tendency is expressed by the appearance of a *new plexus* and a *new girdle* in a *new* position. However, as we have seen in group B, the plexus in the new position does not have the same relation to the girdle-bearing segment that it did in the old; on the contrary, it tends to occupy a place intermediate between such a position and the old one. The girdle also may possibly show a parallel intermediate position; but if so, it is more difficult to verify. Such an intermediate position of the plexus may be interpreted either as representing an atavistic tendency, or an incomplete migration. I am inclined to believe in the latter, and that it indicates a less complete response by the plexus than by the girdle to the influence of the musculature which changes the locus of both girdle and plexus.

The nerve relations in Necturus show that variations of girdle and plexus are nearly parallel, but that these are in some degree independent, as exhibited by the fact that the strength-centre of the plexus does not have just the same relation to the girdle in the variant that it had in the normal condition.

February 20, 1897.

Note. — Since the manuscript of this paper left my hands, two papers bearing upon the question of intercalation have appeared.

Ridewood ('97, p. 366) considers that the point of sacral rib formation and attachment is determined by some stimulus external to the column, and that the girdle does not migrate from one segment to another during ontogeny, — a conclusion which is along the same line as my own (pp. 85, 87).

Baur ('97) contends for intercalation as an ontogenetic process, but I find little in addition to what is contained in his earlier paper (Baur, '91), except that he now (p. 42) supports the idea that the pelvis, developing in one segment, may migrate into a neighboring segment, and become "secondarily united with the vertebral column."

October 1, 1897.

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DESCRIPTION OF PLATES.

The Arabic numerals indicate the serial number of the vertebræ, the Roman numerals the serial number of the ventral branch of the spinal nerves.

ABBREVIATIONS.

br.	Nervus brachialis.	*il-h'ga.*	Nervus ileohypogastricus.
cru.	Nervus cruralis	*isch.*	Nervus ischiadicus.
cst. scr.	Sacral rib.	*prc. t.*	Transverse process.
cst. scr'.	Supernumerary sacral rib.	*su'crac.*	Nervus supracoracoideus.
il.	Ilium.		

All the diagrams are drawn to natural scale of a full grown individual, and are viewed from ventral aspect. The size of nerves is drawn to scale roughly for the average condition.

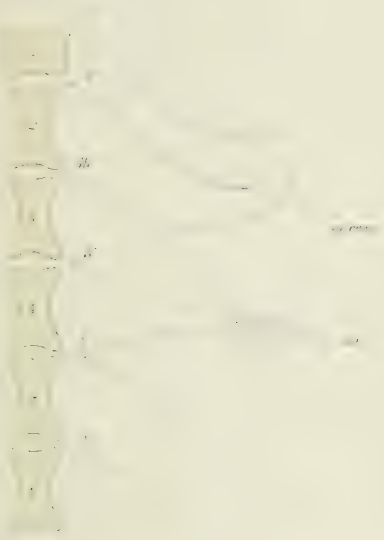
PLATE 1.

Fig. 1. Diagram showing topography of brachial plexus of left side.

Fig. 2. Diagram of lumbo-sacral plexus of left side, as found in α type, group A.

Fig. 3. Diagram of lumbo-sacral plexus of left side, as found in β type, group A.

Fig. 4. Diagram of lumbo-sacral plexus of left side as found in group B.



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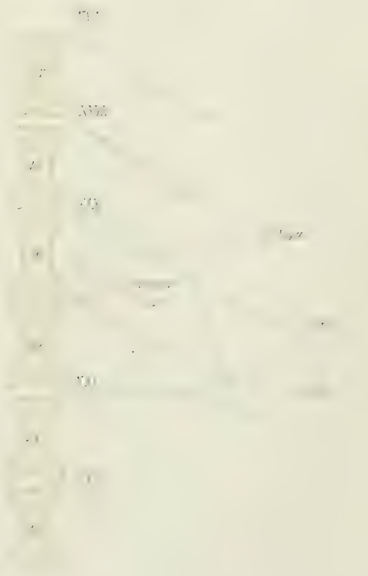

B. Meisel lith Boston

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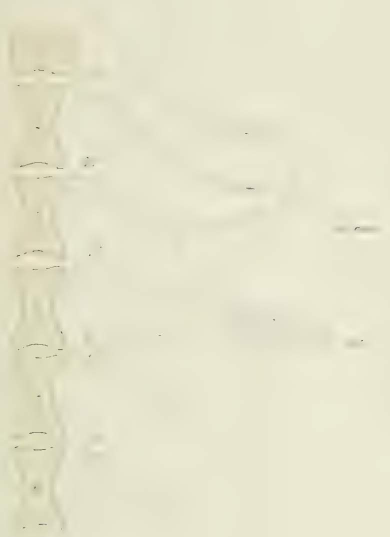

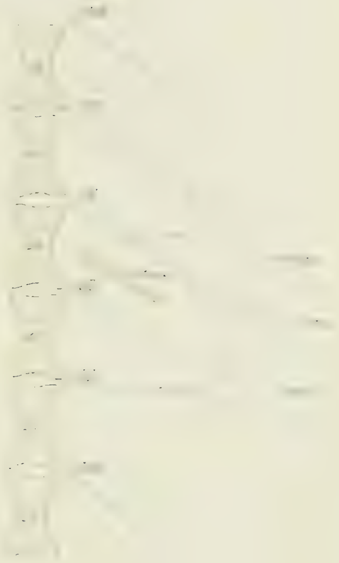

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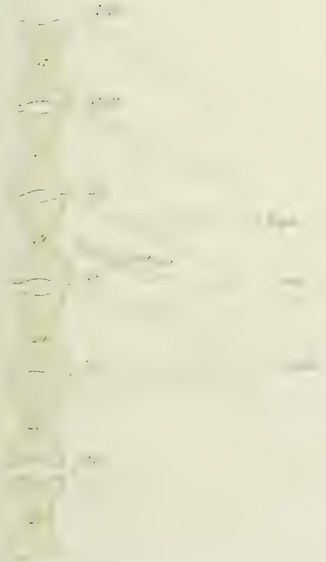

PLATE 2.

Fig. 5. Diagram of plexus of both sides in a specimen bearing asymmetrical sacral ribs on vertebræ 19 and 20.

Fig. 6. Diagram of plexus of both sides of a specimen bearing asymmetrical sacral ribs on vertebræ 18 and 19.

Fig. 7. Diagram showing a bifurcate transverse process and sacral rib.

Fig. 8. Diagram of sacrum of a specimen with a supernumerary sacral rib on one side.

B. Meisel lith. Bost.

No. 5.—*Reports on the Dredging Operations off the West Coast of Central America to the Galapagos, to the West Coast of Mexico, and in the Gulf of California, in charge of* ALEXANDER AGASSIZ, *carried on by the U. S. Fish Commission Steamer "Albatross," during* 1891, Lieut.-Commander Z. L. TANNER, U. S. N., Commanding.

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U. S. Fish Commissioners.]

XXII.

The Isopoda. By H. J. HANSEN.

THE collection contains in all fifteen species, fourteen of which, all marine, I have considered new to science, while one form — belonging to the Oniscidæ — is terrestrial in habit, and proves to be a well known species. Of the fourteen marine species, eight are free-living forms, and one is parasitic on fishes; these nine species are easily referred to genera established many years ago. The remaining five species belong to the subfamily Bopyrinæ, of the very extensive family Epicaridea; they present several peculiarities in structure, and moreover they are rather interesting since no form of the Bopyrinæ has heretofore been found on truly deep-sea animals. For particulars, however, the reader must be referred to the special description later on.

Besides my special account a few remarks must suffice.[1] Since each of the families is represented by only a few species, I am unable to attempt improvements in the classification of any of them. In a previous paper — Isopoden, Cumaceen und Stomatopoden der Plankton-Expedition (Ergebnisse der Plankton-Expedition der Humboldt-Stiftung, Bd. II. G. c) — I have proposed a partly new arrangement of the Isopoda, with observations on some of the families, and to this treatise the reader must be referred for several particulars. I have thought it useful to illustrate all the species rather fully, and to describe them in some detail, taking into consideration the best representations in the literature, yet altering and adding where it seemed advisable.

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[1] The Director of the Entomological Department of the Zoölogical Museum in Copenhagen, Inspector Dr. F. Meinert, had commenced to deal with the material, but being engaged in other work, he transferred to me the preparation of this report. Only the following particulars are of interest. He had recognized the two species of Asellota and all the species of Cymothoidæ as new to science; furthermore, he had furnished them with names, and on the labels briefly mentioned the species already published to which each of the new forms was most closely allied. Some of the names and most of these hints on affinity are adopted in the report, which otherwise is wholly a work of my own. Yet it must finally be mentioned that Mr. G. Budde-Lund has determined the single species of Oniscidæ.

ASELLOTA.

Of this large tribe only two species were secured. Both belong to the Munnopsidæ G. O. Sars, a family rather badly limited, and both must be referred to the genus *Eurycope* G. O. Sars. Unfortunately, the material is rather scanty and all the specimens are much mutilated, yet I am able to draw attention to a point of significance, namely, that the genus with the limits still adopted presents startling differences in the structure and shape of the mandibles of some of the species. In the two species here described the mandibles possess distally a cutting portion, behind this a "lacinia mobilis"[1] with a row of setæ on each mandible and a strong "cuspis laciniæ" on the left one, and farther backward a well developed molar process. In the small Norwegian species the mandibles seem to be of similar structure,[2] but in the large *Eurycope gigantea* G. O. Sars they are very different. In this species each mandible has a very long oblique edge on the inner side, the molar process is very short and badly defined, no lacinia mobilis is found, etc. It may be added that the two pairs of jaws also present differences from those in the species to be described here. (The mouth organs of *Eurycope gigantea* were first described by G. O. Sars in the Norwegian North-Atlantic Expedition, Zoöl., Crustacea, Vol. I. pp. 132, 133, Plate XI. Fig. 10–14, and shortly afterwards by the present author in his account of the Crustacea in Dijmphna-Togtets zool.-bot. Udbytte, 1877, pp. 199–201, Tab. XX. Fig. 3 *c* – 3 *g*.) It is interesting to observe that great differences in the structure and armature of the mouth organs are found in species which in general shape and other structural features seem to be rather closely allied. Unfortunately, the mouth parts in several of the species described by Beddard in the "Challenger" Isopoda are entirely unknown.

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[1] This and the following term are set forth and explained in my paper: Cirolanidæ et Fam. nonn. prop. Musei Haun. (K. Danske Vidensk. Selsk. Skrifter, 6 Række, naturv.-math. Afdeling, V. pp. 239–426, Tab. I.–X.)

[2] At my request, Prof. G. O. Sars very kindly sent me the proof-sheets containing the account of the Munnopsidæ, in his new leading work on the Isopoda. He has divided the family into two families, etc., but he still maintains the genus *Eurycope* in its old and very wide extension, yet remarking that some of the species established by Beddard "ought perhaps more properly to be separated as types of nearly allied genera."

1. **Eurycope pulchra**, n. sp.

Plate I. Fig. 1–1 *i*.

One much mutilated male and six females, three of them with the marsupium well developed, the others much more than half grown or almost fully grown, were captured.

Head. The dorsal surface with three acute processes, the two anterior of which are rather small, each lying a little behind the antennula, while the third odd process is rather good-sized and separated from the two others by a deep and rather broad furrow. On each side this furrow runs down the lateral surface of the head, above it bends obliquely forward, converging with the furrow from the other side, and finally terminating in a median impression between the two anterior processes. The labrum is very large and prominent, anteriorly rounded.

Antennulæ. The basal joint of the peduncle is oblong, anteriorly cut off; the most distal part of the interior side, where the second joint is articulated, is incised; the upper side is irregularly arched, the distal part of the under side longitudinally somewhat excavated. The second joint is as usual short, the next slender and of about the same breadth at both ends; the anterior inner angle somewhat produced, acute. Third joint somewhat shorter and much more slender than the second. The flagellum somewhat exceeding one third of the length of the body, with innumerable joints.

Antennæ. In no specimen are more than the four proximal short joints and sometimes the basal part of the very elongated fifth joint preserved. Third joint anteriorly on the limit between the exterior and the lower side produced into a very conspicuous acute process; the exopod (squama) very small and quite fused with the third joint, not even set off by a transverse suture (compare the following species).

Mandibles (Fig. 1 *b* and 1 *c*). Of about the same shape as in *Janira* and allied genera. The cutting portion (*a*) compressed, much higher (when seen from in front) than broad, ending with three teeth. Pars molaris (*b*) moderately long, somewhat compressed, so that it is broader when seen from in front than when seen from below as in the figure; distally it is cut off obliquely, with some setæ, and as usual the terminal face of the two molar processes is somewhat differently shaped. Lacinia mobilis (*l*) with numerous setæ, and the cuspis lacinia on the left mandible strongly developed, compressed and much higher than broad, ending in four teeth. The palpus stout, three-jointed. Second joint almost double as long as the first; third joint of a peculiar aspect, curved, rather broad, with a conspicuous incision on the anterior margin.

Maxillulæ (Fig. 1 *d*). The lobe (l^1) of the first joint (1) in its distal half rather narrow and curved, with numerous hairs at the rounded apex, but without any spine-like seta. The oblique terminal margin of the lobe (l^3) of the third joint, as in other species, with numerous long spines.

Maxillæ (Fig. 1 *e*). The lobe (l^2) of the second joint proportionally rather narrow, with hairs along the interior margin and on the rounded terminal margin; the two lobes (l^3) of the third joint with some long and robust setæ at the apex.

Maxillipeds (Fig. 1 *f*). Second joint (2) rather long, with about sixteen coupling hooks (*h*) at the inner margin; the terminal margin of its lobe (l^2) coarsely serrated and hairy. Fourth and fifth joints, as in other species, much expanded, but not to such a degree as, for instance, in the following species; the fourth joint conspicuously narrower than the second, and considerably larger than the fifth. Sixth and seventh (7) joints small and slender. The epipod (*ep.*) with a somewhat produced acute angle at the middle of the exterior margin.

Thorax. As usual in this genus, the thorax is divided into two parts, the first of which, consisting of four segments, in this species equals in length the second part. The first segment considerably narrower than the second, the fifth nearly twice as broad as the first. The four anterior segments with a transverse depression in a considerable part of the breadth. The first segment with a single small dorsal process. Second, third, and fourth segments each with a median, very high, laterally compressed, acute dorsal process, turning obliquely forward and rising just behind the anterior margin; besides, the second and third segments with a short rounded protuberance in the median line a little in advance of the posterior margin. The third and the fourth segment with the antero-lateral angle produced into an acute, almost spine-like process; on the first two segments the same angle is rounded. The three posterior segments with a median, longitudinal, rather broad impression, on each side limited by a low keel, anteriorly produced into an acute process, which is long on the fifth and short on the seventh segment. The antero-lateral angle of the three last named segments produced into an acute process, turning forward and somewhat outward, the process being long on the fifth segment, shorter, but almost broader on the last two segments; finally, on the lateral margin a little in advance of the posterior angle, a protuberant rounded process, which is very low on the fifth segment, somewhat larger on the two others, especially on the last one. The whole dorsal surface of the trunk, as of the abdomen, closely set with very small granulations, giving it a faintly scabrous appearance. While the first segment is movably jointed with the head, and the articulation between the four anterior segments, and especially between the fourth and the fifth segment, is very well developed, the three posterior segments are immovably connected with one another and with the abdomen.

Thoracic Legs. The basal joint of the four anterior pairs with the antero-lateral angle produced into a rather good-sized, distally almost spine-like acute process, and laterally with a shorter projecting process; the basal joint of the three posterior pairs smooth. The first pair (Fig. 1 *g*) scarcely of medium length, very slender; the fifth joint almost as long as the second, somewhat curved, very slender, and not expanded on its under side. Of the second, third, and fourth pairs only the two proximal joints are not broken off. In the three last pairs the fifth joint is almost twice as long as broad (Fig. 1 *h*), the seventh joint (7) as long as the fourth, and very slender (in Figure 1 *h* all the hairs are omitted).

Abdomen. As long as the four posterior thoracic segments together, narrower than the seventh segment, and decreasing in breadth from the anterior angle, which is produced into a triangular acute process, turned forward and especially outward. It consists of at least two visible segments — the posterior, of course, consisting of fused segments — fused together, the anterior of which is short; besides, there is seen across the anterior part of the second segment a curved transverse furrow, perhaps indicating a rudiment of a second articulation. In the median line, just behind the furrow between the first segment and the rest of the abdomen, is a small tubercle, especially obvious in a lateral view as a rudimentary process. On the dorsal side are two deep longitudinal furrows, at a considerable distance from each other, and anteriorly curving outward. The posterior margin with three acute processes, the median one curved considerably downward and much larger than the two others, each of which is situated close inside the point where the dorsal furrow reaches the posterior margin. The oblique terminal face of the abdomen is quite similar in both sexes and rather peculiar (Fig. 1 *a* and 1 *i*): the hind margin with the three processes just mentioned, the oblique lateral margin a little arcuate, while the infero-anterior margin is short and concave, the infero-lateral angle being produced into a shorter process; on the upper half of the terminal face are seen the two oblong-triangular anal doors (Fig. 1 *i*, *d*), and just outside each door the uropod is attached. In the female the ventral operculum (the first pair of abdominal limbs) has an impression along with and somewhat inside of the lateral margin and close to the posterior margin; in the median line it possesses a keel, which somewhat before the middle is produced into a rather long, moderately compressed acute process. In the male the operculum (the first and second pairs of abdominal limbs together) is represented in Figure 1 *i*, and scarcely needs a special description. (Having but one male specimen, I omit the description of the "appendix masculina" on the second limb.)

Uropods (Fig. 1 *i*). Each consists of a moderately short and very slender peduncle and two 1-jointed rami, the interior of which is about as long as the peduncle and still more slender, the exterior one somewhat shorter.

Size. A female specimen whose marsupium is still rudimentary (consisting only of small plates on the second and fourth pairs of legs) is 28 mm. long and 11.2 mm. broad. Of the three females with the marsupium completely developed (in two specimens filled with eggs) the largest is a little smaller than the specimen with rudimentary marsupium; the smallest is 23.3 mm. long and 9.8 mm. broad. The youngest female is 20.3 mm. long; the male is about 24.5 mm. long and 10 mm. broad.

Habitat. Station 3361 (Lat. 6° 10′ N., Long. 83° 6′ W.), 1471 fathoms, 2 specimens; Station 3413 (Lat. 2° 34′ N., Long. 92° 6′ W.), 1360 fathoms, 5 specimens.

Remarks. This species is closely allied to *Eurycope fragilis* Bedd. ("Challenger" Isopoda, p. 63, Plate XI. Fig. 8–12); but if the drawings of Beddard are trustworthy in detail, my species is easily distinguished from *E. fragilis* by the processes on the dorsal surface of the head, by the shape of the lateral margin of the three posterior thoracic segments, by the direction of the postero-lateral abdominal processes, etc. However, a thorough revision of many of the "Challenger" Isopoda, especially of the Asellota (sens. lat.), is very much needed.

2. Eurycope scabra, n. sp.

Plate I. Fig. 2–2 *d*; Plate II. Fig. 1.

Only one single and ill-handled female specimen is present; yet I hope that the species can be easily recognized, especially by the aid of my figures.

Head, thorax, and *abdomen* without any processes, and scarcely with sharp angles; but with the exception of a transverse belt across each of the four anterior thoracic segments, the dorsal surface of the body is almost wholly covered with numerous granulations, so that it becomes scabrous in a much higher degree than the preceding species.

Antennulæ. Absent.

Antennæ. Only the four proximal joints are present. The third joint without any process, but above at the exterior side is seen a small triangular and rounded exopod, well set off by a suture.

Mandibles. Only the left mandible (Fig. 2 *a*) has been examined. The cutting portion well developed, ending in five teeth; the lacinia with about six setæ, and the cuspis laciniæ large, with teeth of very different magnitude. The molar process rather long and proportionally slender, seen from below (as in Fig. 2 *a*) almost conical with the end cut off very obliquely; seen from in front the distal part is somewhat broader, and the terminal face is vertical, with sharp serrulation and a few broad hairs; but in the lower end of the face a triangular process is seen, and it is this process which in Figure 2 *a* overlaps the greater part of the end. The palp is very slender; second joint but a little longer than the first; the third very slender.

Maxillulæ (Fig. 2 *b*). The distal part of the lobe of the first joint broader and less curved than in the preceding species, hairy and without spine-like setæ; the lobe of the third joint about as in *Eurycope pulchra.*

Maxillæ (Fig. 2 *c*). The lobe of the second joint distally proportionally narrow and tapering towards the rounded apex, which is furnished with normal hairs.

Maxillipeds (Fig. 2 *d*). Second joint rather elongate, its lobe with the terminal margin closely serrated and with about twelve coupling-hooks at the inner margin. Fourth and fifth joints more expanded than in *Eurycope* *pulchra*, the fifth almost as large as the fourth, and its inner margin partly serrated; sixth and seventh joints much broader than in the preceding species. The epipod with the exterior margin evenly curved.

Thorax. It was badly preserved, and therefore the relative breadth of the segments could not be drawn with so much certainty as could be wished. The want of processes and the scabrous surface are mentioned above. The three posterior segments, without any median dorsal impression not connected immovably with each other, and somewhat shorter than the four others together; the last segment seems to be movably united with the abdomen.

Thoracic Legs. The basal joint of the four anterior pairs anteriorly or exteriorly produced into an angle or short scabrous process. The first pair (Plate II. Fig. 1) rather short and stout; the fifth joint conspicuously shorter than the second, compressed and somewhat expanded on the under side, the margin of which is hairy. Of the six other pairs of legs only the basal joint is preserved.

Abdomen. It is nearly ovate and proportionally large compared with the thorax, but neither shape nor magnitude could be drawn with absolute certainty, as the abdomen was roughly handled. The basal segment is very short; for the rest only a pair of very faint somewhat curved longitudinal impressions are seen on the scabrous dorsal surface. The operculum in the female without any keel.

Uropods. Somewhat longer than in the preceding species, but of about the same shape.

Size. The specimen described is about 25.6 mm. long, and 8.4 mm. broad.

Habitat. Station 3413 (Lat. 2° 34′ N., Long. 92° 6′ W.), 1360 fathoms, 1 specimen.

Remarks. It is easily distinguished from all other large species hitherto known by the general shape of thorax and abdomen, and the want of processes.

CYMOTHOIDÆ.

As to the limitation and the constituent elements of this family I refer to the above named report on the Isopoda of the German Plankton Expedition. Of its six sub-families only two, namely, Æginæ and Cymothoinæ, are represented in the collection, the first sub-family by six, the second by one species. The leading work on these two sub-families is Shiödte and Meinert: Symbolæ ad Monogr. Cymothoarum, Crust. Isopod. Familia (Naturh. Tidsskr., 3 R., Bd. XII.–XIV., 1879–84), and further remarks on the structure of the mouth and the classification are found in my above named work, Cirolanidæ, etc.

In the large genus *Æga* Leach, not rarely several species are closely allied to one another, and three of the four species established here differ only in small features from species living in the most northern part of the Atlantic (in Norway, Greenland, etc.). In the following, some characters derived from the structure of the thoracic legs, and partly overlooked by earlier authors, will be used; besides, the shape of the posterior angles of the thoracic "epimera," of the sixth abdominal segment, and especially of the uropods, furnish us with more distinguishing marks than are generally recognized, but as most of these details are more easily apprehended from figures, I will direct the attention of future students to these facts, believing that proportionally rather large and very accurate drawings of the parts mentioned will be extremely useful.

In specimens of Æginæ taken on fishes, the ventral side of the thorax is often, nay almost generally, vaulted, and sometimes very considerably so, owing to the fact that the alimentary canal is greatly distended by blood sucked from the host; another result of this swollen condition is that the segments of the thorax very often become drawn out from each other. In specimens taken on the bottom of the sea by trawl or dredge, the ventral side is not vaulted, and the thoracic segments are not drawn out, it follows that such specimens are comparatively shorter in proportion to their breadth than most of the specimens taken on fishes, and therefore present a somewhat different aspect. No specimen of the Æginæ in this collection has the ventral side vaulted, and all seem to be taken on the bottom.

Schiödte and Meinert divide the species of the genus *Æga* into two groups. The first of them is thus diagnosed: "Scapi antennarum infra plani vel concavi, invicem accommodati. Lamina frontalis plana vel concava," and to this group the two first described species, *Æ. maxima*, n. sp., and *Æ. acuminata*, n. sp., must be referred. To the other group the two authors ascribe the following characters: "Scapi antennarum teretiusculi vel compressi, invicem liberi. Lamina frontalis convexa vel compresse elevata," and to this belong the two other species, *Æ. plebeia*, n. sp., and *Æ. longicornis*, n. sp.

3. Æga maxima, n. sp.

Plate II. Fig. 2–2 *c*.

Only one specimen, a female without marsupium.

Head. The frontal margin rather concave on each side; the median elongation acute, reaching to about the middle of the interior margin of the first joint of the antennulæ. The frontal plate "lamina frontalis" (on the ventral side of the head), about as long as broad, seen as much as possible from the side considerably convex, and seen from in front with a low and rather broad sublateral carina, and somewhat excavated in the middle. The eyes ovate, the shortest distance between them only a little less than the basal joints of both antennulæ together.

Antennulæ. Reaching very little beyond the end of the peduncle of the antennæ, and a little beyond the anterior angle of the first thoracic segment. The peduncle very little longer than the flagellum; its basal joint as long as broad, with the upper side flatly convex, and the antero-interior angle rectangular. The flagellum 17-jointed.

Antennæ. Each antenna, when bent backward, nearly attains the posterior margin of the second thoracic segment. The proportion between the peduncle and the flagellum is about that of 3 to 5; the flagellum 23-jointed.

Thorax (Fig. 2 *a*). The posterior angle of the first segment rectangular, scarcely produced. For practical reasons, the "epimera" of the six following segments, though in reality constituting the first joint of the legs, are here treated as belonging to the thorax ; the epimera of the second thoracic segment with the posterior free angle nearly rectangular, those of the third segment somewhat obtuse-angular. The epimera of the four posterior segments posteriorly considerably produced ; those of the fourth and fifth segments posteriorly obliquely rounded ; the last two pairs with the triangular apex a little rounded.

Thoracic Legs. All clumsy. In the three anterior pairs the fourth joint (the epimeron considered as the first joint) is shorter than the third, considerably incrassated, in the first pair with only one spine, in the second with six or seven (Fig. 2 *b*), in the third with nine short spines at the interior margin ; the fifth joint only in the third pair with a spine at the antero-interior angle ; the sixth joint short, without keel on the inner side; the claw (consisting of the seventh joint fused with the real claw) short and robust. The four posterior pairs (Fig. 2 *c*) with numerous, comparatively short spines.

Abdomen. The first segment partly free, a little broader than the fourth. The sixth segment about $1\frac{1}{2}$ times broader than long; the dorsal surface feebly convex, very slightly keeled in the median line, and between this keel and the base of the uropod is seen a large, but shallow depression; as the posterior apex unfortunately is broken off, nothing can be said about its shape, but most likely it was acute, and the posterior margin probably with about five spines on each side.

Uropods. They reach a little beyond the end of the abdomen ; both rami are proportionally narrow, of the same breadth and the same length, the inner ramus therefore posteriorly surpassing the outer one. The inner ramus more than three times longer than broad; the interior margin from a point a little behind the apex of the very long and narrow process from the peduncle turning obliquely outward, thus forming a posterior margin, with five or six small spines ; the exterior margin somewhat convex, but at a short distance from the rounded tip of the branch it changes its direction, bending somewhat outward, thus forming a low incision. The outer ramus with the tip rounded; the distal part of both margins faintly serrated with a smaller number of spines.

Color. The whole dorsal surface yellowish white, the eyes grayish.

Size. The single specimen measures 55 mm. in length and 26 mm. in breadth.

Habitat. Station 3362 (Lat. 5° 56′ N., Long. 85° 10′ 30″ W.), 1175 fathoms, 1 specimen.

Remarks. The species is closely allied to *Æ. psora* (L.), but is easily distinguished by its enormous size, and the following characters : a different shape of the frontal plate; the eyes smaller and more distant from each other ; the dorsal surface of the last abdominal segment slightly convex, with two large depressions.

4. **Æga acuminata,** n. sp.

Plate II. Fig. 3–3 *b*.

Only one specimen, a female without marsupium.

Head. The frontal margin scarcely as concave on each side as in *Æ. maxima*, the median elongation not reaching the middle of the interior margin of the first joint of the antennulæ. The frontal plate conspicuously broader than long, seen from the side shaped as in the preceding species, seen from in front somewhat concave with projecting lateral margins. The eyes as in the preceding species.

Antennulæ (Fig. 3). Reaching considerably beyond the peduncle of the antennæ, to the middle of the first thoracic segment. The peduncle slightly shorter than the flagellum; the basal joint, seen from in front, quite as broad as long; the dorsal surface somewhat convex; the antero-interior angle a little produced, acute-angled. The flagellum 18-jointed.

Antennæ. When reflexed, reaching to the posterior margin of the second thoracic segment. The relation of the peduncle to the flagellum is about that of 2 to 3; the flagellum 19–20-jointed.

Thorax (Fig. 3 *a*). The posterior margin of the epimera of the second to the fifth segment and the corresponding margin of the first segment sinuate, being directed a little forward just inside the somewhat produced postero-lateral angle, which is scarcely rectangular, but a little acute-angled. The epimera of the sixth segment forming a transition between those of the fifth and of the seventh segment, the last named pair posteriorly and laterally considerably produced and acute.

Thoracic Legs. They are robust, though scarcely as clumsy as in *Æ. maxima*, but very similar in shape and armature. In the three anterior pairs the claw is somewhat longer; the thick fourth joint in the first pair with one spine, in the second with five, in the third with six to eight spines. The spines on the four posterior pairs scarcely as numerous as in the preceding species, but somewhat longer.

Abdomen. The first segment almost totally covered, very conspicuously broader than the fourth. The last segment scarcely $1\frac{1}{3}$ times broader than long (in Fig. 3 *b* it seems to be proportionally broader, owing to the circumstance that the figure presents the projection of the posterior segments); posteriorly it is considerably produced, acute, with about three spines on each side of the tip; the dorsal surface is rather convex, median keel and sublateral depressions scarcely visible.

Uropods (Fig. 3 *b*). Much as in *Æ. maxima*, so that only the more essential differences will be pointed out. The outer ramus reaching a little beyond the inner one; the inner ramus is more deeply incised on the exterior side, and the posterior margin is somewhat longer: thus we obtain a distal part forming an obtuse angle with the larger proximal part.

Color. The dorsal surface is light yellowish gray with a faint purple tone on a part of the three anterior thoracic segments, and the last abdominal segment yellowish white; the eyes dark grayish, almost black.

Size. The single specimen is 31 mm. long, 16.2 mm. broad.

Habitat. Station 3403 (Lat. 0° 58′ 30″ S., Long. 89° 17′ W.), 384 fathoms, 1 specimen.

Remarks. The species is very closely allied to *Æ. psora* (L.), but is distinguished especially by smaller eyes, longer antennulæ, and the last abdominal segment being posteriorly more produced. From *Æ. maxima* it is distinguished especially by longer antennulæ, and by a different shape of the last abdominal segment and of the uropods.

5. Æga plebeia, n. sp.

Plate II. Fig. 4–4 *d*.

Six specimens, one male and five females, three of the latter with well developed marsupium.

Head. The frontal margin with the sub-median curves rather indistinct; the median process extends a little below the inferior edge of the antennulæ, its apex almost or quite reaching the frontal plate. The frontal plate about twice as broad as long and strongly compressed, forming a high tranverse keel, which, seen from in front, shows the shape of the half of an oval. The eyes (Fig. 4) are very large; the distance between them considerably shorter than the breadth of the frontal process.

Antennulæ. Much longer than the peduncle of the antennæ (Fig. 4), and bent backwards, reaching almost to or even beyond the posterior angle of the first thoracic segment. The peduncle is somewhat shorter than the flagellum, and almost attains the distal end of the penultimate joint of the peduncle of the antennæ; the first joint is about as long as broad, with the antero-interior angle broadly rounded; the third joint of the peduncle as long as, or a little longer than, the two proximal joints together. The flagellum with twenty-one to twenty-three joints.

Antennæ. They reach a little beyond the posterior margin of the second, or almost to the posterior margin of the third thoracic segment. The flagellum $1\frac{1}{3}$ or $1\frac{1}{2}$ times longer than the peduncle, with seventeen or eighteen joints.

Thorax (Fig. 4 *a*). The postero-lateral angle of the first segment rectangular or a little acute, that of the epimera of the second and generally of the third segment conspicuously produced and acute; the angle of the fifth and sixth epimera almost or quite rectangular. The epimera of the seventh segment somewhat produced and acute.

Thoracic Legs. The three anterior pairs slender and rather long: the fourth joint not incrassated, with concave interior margin (Fig. 4 *b*), and with a couple of small spines at the distal inner angle; the sixth joint rather long, with a strong spine on the interior margin near the end; the claw very long, and longer than the sixth joint. The four posterior pairs are slender; the fourth joint elongate, and considerably longer than the fifth.

Abdomen. The first segment partly covered, very conspicuously broader than the fourth. The last segment (Fig. 4 *d*) $1\frac{1}{4}$ times broader than long; the tip acute, but scarcely produced; the posterior margin with six to eight small serratures, with scarcely visible spines on each side of the apex; the dorsal surface slightly convex, the faint median keel and the sub-lateral impressions almost as in *Æ. maxima* (see *supra*).

Uropods (Fig. 4 *d*). They reach somewhat beyond the apex of the abdomen, the outer ramus almost or quite attaining the end of the inner one. The inner ramus relatively broad, scarcely half as broad as long, of a somewhat triangular shape; the posterior margin considerably shorter than the antero-interior one, with seven or eight rather fine serratures; the exterior margin with a break at some distance from the acute tip, and two or three serratures between the tip and the break, the rest of the margin almost straight and smooth. The outer ramus is conspicuously narrower than the inner, yet rather broad, the apex acute, not produced.

Color. The dorsal surface yellowish white, the eyes gray, somewhat blackish.

Size. The largest specimen, a female with marsupium, is 37 mm. long and 17 mm. broad; the smallest female with marsupium is but 22 mm. long; the single male is 23.4 mm. long and 10.5 mm. broad.

Habitat. Station 3363 (Lat. 5° 43′ N., Long. 85° 50′ W.), 978 fathoms, 4 specimens; Station 3371 (Lat. 5° 26′ 20″ N., Long. 86° 55′ W.), 770 fathoms, 1 specimen; Station 3402 (Lat. 0° 57′ 30″ S., Long. 89° 3′ 30″ W.), 421 fathoms, 1 specimen.

Remarks. The species is closely allied to *Æ. ventrosa* M. Sars, but in the last named species the frontal plate is lower and of another shape, the eyes are more narrow, not occupying so much of the dorsal surface of the head, the epimera of the sixth, and especially those of the seventh segment are considerably more produced, and the outer ramus of the uropods is somewhat broader.

6. **Æga longicornis**, n. sp.

Plate II. Fig. 5-5 *b*; Plate III. Fig. 1-1 *a*.

Only one specimen, a female without marsupium.

Head. The frontal margin with the sub-median curves rather faint; the median process as in the preceding species. The frontal plate forms a very high transverse keel, which, when the head is seen from in front, protrudes strongly beyond the basal parts of the antennulæ and the antennæ, and has a straight inferior margin and rounded lateral angles. The eyes (Fig. 5) comparatively narrow, the shortest distance between them a little shorter than the basal joint of both antennulæ and the breadth of the frontal process together.

Antennulæ. They reach considerably beyond the peduncle of the antennæ, and almost to the postero-lateral angle of the first thoracic segment. The peduncle a little shorter than the flagellum; its basal joint about as long as broad, with the antero-interior angle broadly rounded, the third joint scarcely shorter than the two proximal joints together. The flagellum with about fifteen joints.

Antennæ. They are unusually long, reaching to the middle of the fifth thoracic segment. The flagellum more than twice as long as the peduncle, with twenty-two joints.

Thorax. The postero-lateral angle of the first segment and of the epimera of all the other segments acute and more or less acute-angled (Fig. 5 *a*).

Thoracic Legs. The three anterior pairs are slender and rather long (Plate III. Fig. 1); their fourth joint scarcely incrassated, with concave inner margin, and in the second and third pairs with a couple of spines at the distal inner angle; the sixth joint rather long and without spines; the claw rather long, but scarcely longer than the sixth joint. The four posterior pairs rather long and slender (Plate III. Fig. 1 *a*); the fourth joint a little shorter, or at all events not longer, than the fifth.

Abdomen. The first segment almost covered, and very conspicuously broader than the fourth. The last segment (Fig. 5 *b*) about 1⅓ times broader than long; the apex acute but very little produced; the posterior margin on each side of the apex with four or five comparatively coarse serratures, and a conspicuous spine in each incision; the dorsal surface very flatly convex, with a transverse depression near the base and the median keel not discernible.

Uropods (Fig. 5 *b*). They reach far beyond the apex of the abdomen, the inner ramus scarcely attaining the end of the outer one. The inner ramus is relatively broad, but yet more than twice as long as broad, triangular, the triangle being almost isosceles, with rounded vertex, as the posterior margin is almost as long as the antero-interior one; the exterior margin almost straight, with about five coarse serratures in the distal half, and the posterior margin is also serrated; the apex is acute. The outer ramus much narrower than the inner one, about four times longer than broad; the apex much produced, acute.

Color. The dorsal surface is yellowish white, the eyes black.

Size. The single specimen is 14.5 mm. long and 7.5 mm. broad.

Habitat. Station 3402 (Lat. 0° 57′ 30″ S., Long. 89° 3′ 30″ W.), 421 fathoms, 1 specimen.

Remarks. The species is easily distinguished by the following characters together: the long distance between the eyes, the long antennæ, and the relative length of the rami of the uropods.

7. **Rocinela laticauda**, n. sp.

Plate III. Fig. 2–2 *e*.

Three specimens of very different size, one a large and in all probability adult male; no female with marsupium.

Head.[1] The eyes of medium size, the shortest distance between them about as long as the last joint of the peduncle of the antennæ; the distance in the smallest specimen is comparatively a little shorter than in the largest one.

Antennulæ. They surpass a little the middle of the last joint of the peduncle of the antennæ (Fig. 2 *a*); the peduncle reaching a little beyond the extero-anterior angle of the third joint of the peduncle of the antennæ; the flagellum in the small specimen with five, in the large specimens with six joints.

Antennæ. They reach a little beyond the middle of the third thoracic segment; the flagellum in the small specimen with fifteen, in the two other specimens with sixteen joints.

Thorax. The epimera (Fig. 2 *b*) of second and third thoracic segments posteriorly rounded and not produced, those of the fourth segment somewhat produced with rounded apex, those of the three posterior segments considerably produced and almost acute.

Thoracic Legs. The three anterior pairs (Fig. 2 *c*) tolerably stout: the fourth joint with about four acute spines, some of them rather long; the sixth joint quite as broad as the fourth, its large and broad expansion on the inner side with six spines. The four posterior pairs (Fig. 2 *d*) with numerous slender spines.

Abdomen (Fig. 2 *e*). The first segment is entirely concealed under the last thoracic one. The abdomen increases very conspicuously in breadth from the second to the fourth segment. The last segment is large and broad, posteriorly very broadly rounded; the dorsal surface is keeled anteriorly in the middle, and from the keel towards the lateral margin it is rather deeply, or, in the two smaller specimens, deeply and broadly depressed, the depression not reaching the lateral margin; the posterior margin with a number of very small spines.

Uropods (Fig. 2 *e*). They surpass a little the last abdominal segment. The outer ramus reaches very little beyond the inner one, is considerably, but not 1½ times, broader than this, and is furnished with a number of spines on a larger part of its exterior margin. The inner ramus with spines on the terminal margin, and on the larger part of the outer margin.

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[1] Schiödte and Meinert write (Nat. Tidsskr., 3 R., Bd. XII. p. 383) on the species of the genus *Rocinela*: "Bene recordari debet, discrimen, quod individua speciei unius ejusdemque quoad figuram frontis atque sculpturam partis prioris trunci præbent, non sexum, sed ætatem diversam notare." This observation is a very valuable one, as the differences in the front sometimes lead to great confusion. The frontal plate seems to be very small in all species; the thoracic epimera show much smaller differences in the various species than in the species of *Æga*.

Color. The two smaller specimens yellowish white, with a reddish tone on a part of the three anterior segments, and the eyes blackish; the large specimen is more grayish, posteriorly on the dorsal surface of the last abdominal segment and on a part of the uropods reddish brown, the eyes black.

Size. The largest specimen, a male, is 40.5 mm. long, and 16 mm. broad; the two other specimens are immature females, the smallest of them 21 mm. long.

Habitat. Station 3418 (Lat. 16° 33′ N., Long. 99° 52′ 30″ W.), 660 fathoms, 1 specimen; Station 3425 (Lat. 21° 19′ N., Long. 106° 24′ W.), 680 fathoms, 1 specimen; Station 3430 (Lat. 23° 16′ N., Long. 107° 31′ W.), 852 fathoms, 1 specimen.

Remarks. The species is closely allied to *R. australis* Sch. & Mein., but in this last species the eyes are very conspicuously larger and the distance between them considerably shorter than the last joint of the peduncle of the antennæ, the abdomen does not increase in breadth from the base to the fourth segment, the last abdominal segment is somewhat smaller and the outer ramus of the uropods much broader, about $1\frac{2}{3}$ times broader than the inner ramus.

8. Rocinela modesta, n. sp.

Plate III. Fig. 3–3 *c*.

Only one somewhat mutilated specimen, a female with marsupium.

Head. The eyes are rather small, occupying only about half of the lateral margin of the head, and the distance between them considerably longer than the last joint of the peduncle of the antennæ.

Antennulæ (Fig. 3). Comparatively long, reaching very little beyond the peduncle of the antennæ. The peduncle surpasses the middle of the penultimate joint of the peduncle of the antennæ. The flagellum with six joints.

Antennæ. In my single specimen only the peduncles are present.

Thorax. The epimera essentially as in the preceding species, yet posteriorly a little more produced.

Thoracic Legs. The first three pairs (Fig. 3 *a*) of medium size, rather slender: the fourth joint with from three to four blunt spines; the sixth joint not as broad as the fourth, the expansion on the inner side rather low and short, with four feeble spines. The four posterior pairs (Fig. 3 *b*) nearly as in the preceding species, but the spines are less numerous.

Abdomen (Fig. 3 *c*). The first segment is completely covered; the second quite as broad as the fourth. The last segment is smaller than in the preceding species, decreasing considerably in breadth from before the middle backward; posteriorly it is comparatively rather narrow and rounded, with some few fine spines on each side of the median line; the dorsal surface is somewhat convex, keeled anteriorly in the median line and with a rather deep but not broad depression from that keel outwards almost to the lateral margin.

Uropods (Fig. 3 *c*). The inner ramus surpasses a little the abdomen and very little the outer ramus, which is somewhat broader than the other; both rami with rather feeble spines on the major part of the exterior margin; the inner ramus with some spines on the obliquely rounded terminal margin.

Color. The dorsal surface is whitish, the eyes dark.

Size. The single specimen, a female with marsupium, is 23.5 mm. long, and 10.7 mm. broad.

Habitat. Station 3384 (Lat. 7° 31′ 30″ N., Long. 79° 14′ W.), 458 fathoms, 1 specimen.

Remarks. This species is closely allied to *R. maculata* Sch. & Mein., but it totally lacks the four large black spots; furthermore, in the last named species the uropods are a little shorter and broader, and the two rami of equal breadth, while the outer ramus is conspicuously shorter than the inner one; the three anterior pairs of legs are relatively shorter and more clumsy, etc.

9. Irona foveolata, n. sp.

Plate III. Fig. 4–4 *b*.

Seven specimens, all females with marsupium, were secured. The species certainly must be referred to the genus *Irona* Sch. & Mein., but as in my opinion it would be of little value to work out a long and very detailed account, I prefer to give a shorter description, especially pointing out the features by which it is distinguished from the four species described by Schiödte and Meinert in their monograph (Nat. Tidsskr., 3 R., Bd. XIV. pp. 383–395), and more particularly from *Irona melanosticta* Sch. & Mein., to which it is rather closely allied. As in adult females of other species belonging to *Irona*, *Lironeca*, etc., the body is unsymmetrical and somewhat variable in shape, in some specimens being contorted to the right, in others to the left side; furthermore, the last abdominal segment is sometimes as large as shown in the drawing (Fig. 4), sometimes a little larger or smaller, in the smallest specimen even conspicuously smaller.

The body is about twice as long as broad, in the smallest specimen a little shorter and broader, much depressed, but the dorsal surface of the thorax and the median part of the five anterior abdominal segments yet more or less but never strongly vaulted, while the lateral part of the abdominal segments mentioned and the whole sixth abdominal segment are nearly or quite flat, but sometimes obviously contorted.

Thorax. The epimera of the second, third, and fourth thoracic segments are very narrow, seen from above; those of the fifth segment a little broader and posteriorly more produced. The epimera of the sixth and especially of the seventh segment are much broader and posteriorly much more produced than the others, besides on each side rising considerably above the more lateral part of the dorsal surface of the thorax, which is brought about by the curious fact that these epimera are turned outwards and somewhat upwards.

Abdomen. All the segments are very broad. The last segment either rather thin and tolerably large, or mostly, as in Figure 4, thin and very large, and in this instance almost membranous, so that the marginal part easily becomes folded. The dorsal surface of this last segment sometimes with tolerably distinct, sometimes with very faint median keel, and else almost all over finely and densely pock-marked by exceedingly numerous and very small depressions. (This structure is not clearly defined on the copperplate, as the depressions are far more numerous than in the figure, and the intervals form a kind of irregular reticular work.)

Uropods. They have a very depressed peduncle and thin rami; the outer ramus is oblong-ovate, distally rounded; the inner ramus is considerably longer than the outer, with sub-acute end.

Color. In the six larger specimens the head, the thorax, the five short abdominal segments, and the basal part of the sixth segment, are yellowish with innumerable dark dots; the epimera of the three, and especially of the two, posterior thoracic segments, and the lateral angles of the five anterior abdominal segments are white; almost the whole last abdominal segment is grayish. In the smallest specimen the dorsal surface is darker, more grayish, with exception of the two last pairs of thoracic epimera and the angles of the five anterior abdominal segments, which are white.

Size. The largest specimen is 20.5 mm. long, and 10.5 mm. broad; the smallest is 14.5 mm. long, and 8.2 mm. broad.

Habitat. Station 3355 (Lat. 7° 12′ 20″ N., Long. 80° 55′ W.), 182 fathoms, 2 specimens; Station 3389 (Lat. 7° 16′ 45″ N., Long. 79° 56′ 30″ W.), 210 fathoms, 4 specimens; Station 3391 (Lat. 7° 33′ 40″ N., Long. 79° 43′ 20″ W.), 153 fathoms, 1 specimen. On the labels I do not find any mention of the name or names of the fishes on which the parasites must have been found.

Remarks. The species seems to be well distinguished, especially by the pock-marked surface of the last abdominal segment. No males were found. In the marsupium of one female I found "pullus stadii primi" of Schiödte and Meinert; in Figure 4 *a* a leg of the second pair, and in Figure 4 *b* the posterior abdominal segments and the uropods of one of the specimens are shown. This may be sufficient, as the young one in this stage is very similar to those of the genus *Lironeca* drawn by Schiödte. Unfortunately, the "pullus stadii secundi," always much more interesting, was not found.

EPICARIDEA.

As to the division of this very rich and highly interesting family into sub-families the reader is referred to my above mentioned treatise on the Isopoda of the Plankton Expedition. Of the four sub-families admitted (the very doubtful Microniscinæ not included) only one, viz. the Bopyrinæ, is represented in the collection. Of the five species secured both female and male — but no young ones — are present of the four species, while the fifth species is represented only by a male and a small portion of a female.

It is a rather unpleasant task to describe a few new forms of the Bopyrinæ. Most of the authors who have contributed to the knowledge of the group possessed very few species, and often even very few specimens, and the animals being not very easy to examine, and still less to describe and draw, the result is that most of the species are imperfectly represented, and many of the genera badly or not at all limited. Giard and Bonnier have given full descriptions of a few species only, as their principal work on this sub-family has not yet been published. They have made an attempt to divide the Bopyrinæ into three groups, Phyxiens, Bopyriens, and Ioniens; but I am unable to perceive the limits between the two first named groups, and even the group Ioniens is not very sharply defined. We must wait until a number of still unknown forms have been thoroughly studied and many of the already established species reexamined before it will be possible to divide the sub-family into natural groups. I must add, however, that the few descriptions just mentioned of the two authors have been very useful to me. In 1893, T. R. R. Stebbing, in his well known work, "A History of Crustacea — Recent Malacostraca," gave a very good catalogue of all the twenty-one genera and almost all the species hitherto established.

I must confess that I have been unable to refer more than one of my five new species to any of the genera hitherto established, and as they are very different from one another it is necessary to institute four new genera, — a result with which I am rather dissatisfied, not being sure that they all will prove to be valid. On account of the present state of things, I do not venture to lay down diagnoses of the new genera; but I hope that by means of my rather numerous figures and tolerably full descriptions it will be easy not only to recognize my species, but also to place the genera properly and work out the diagnoses, when in the future we get a real systematic arrangement.

10. **Cryptione elongata**, n. gen., n. sp.

Plate III. Fig. 5–5 *a*; Plate IV. Fig. 1–1 *g*.

A fine female with its male (Fig. 1 *a*, *m*) was discovered.

a. *Female.*

The body is elongate (Fig. 1) and (the uropods not included) about twice as long as broad; the greatest breadth at about the middle.

Head. It forms, when seen from above (Fig. 1), almost a regular transverse oval, with the anterior half projecting in advance of the antero-lateral part of the thorax and the frontal margin considerably and evenly curved; the dorsal surface somewhat convex, with a depression a little inside of the anterior margin. The antennulæ (Fig. 1 *b*, *a*) rather distant from each other, of medium size, 3-jointed; the basal joint is considerably enlarged, the terminal joint minute. The antennæ (*b*) rather long, 3-jointed; the basal joint very large, ovate, with the second joint proceeding from the extero-anterior part; the second joint relatively rather long and robust (compare the following forms), the third somewhat shorter and considerably more slender. A frontal plate is absent, and between the antennulæ, the antennæ, and the labrum is found a rather large free space. The labrum (*c*) is tolerably small, a little broader than the hypopharynx, the posterior margin emarginate. The hypopharynx (*h*) with the lateral margins sub-parallel. Mandibles (*d*), maxillulæ (*e*), and maxillæ (*f*) scarcely need special mention, their general shape and position being easily seen in Fig. 1 *b*. In this figure the place of attachment of the maxillipeds is lettered with *g*. The left maxilliped, seen from below, is shown in Figure 1 *c*; the first joint (1) with its usual free posterior dilatation, the second joint (2) with the exterior dilatation (d^2) which is of secondary origin — as in the females of the family Cymothoidæ — and cannot be considered as an exopod; the palp (*p*) is longer than in the following forms, but not distinctly jointed. The peculiar border behind the attachment of the maxillipeds is well developed, having on each side two oblique, good-sized rather broad, but not long, somewhat fleshy, lamellar processes (Fig. 1 *b*, *l*).

Thorax. On the four anterior segments the ovarian bosses are well developed, occupying but a little more than half the length of the sub-marginal part of each segment; in the other segments the bosses are wanting. The pleural plates (" lames pleurales " of Giard and Bonnier) of the four anterior segments are interesting: each of them is divided by a deep incision into two portions, the anterior of which is oblong, set off by a furrow and especially on the right side of the animal incised or emarginate exteriorly, while the posterior forms a shorter, rounded, not defined lobe. In the three posterior segments the pleural plates are larger and laterally more prominent, but neither divided nor set off. The ventral side of the two posterior segments is elevated and divided by numerous longitudinal ridges into low fleshy lamellæ; the other segments possess a similar, but more narrow, transverse keel divided into small protuberances. The legs are normal, each sitting on an eminence which often is rather prominent (its appearance on the left side of the figure conveys the impression that the leg has a short basal joint, which of course is not the case); the second joint (basipodite, Giard and Bonnier, the basal joint being fused with the segment) not expanded; the claw is present, and none of the joints with keels or rugosities. The first left leg with its marsupial plate is exhibited in Figure 1 *d*, which, better than a long description, will show the differences between the plate in this and in the following forms; the transverse furrow on its exterior side is plainly seen, and on the inner side is found a transverse keel, the proximal part of which is divided into a few lamellæ. The margins of the marsupial plates are more or less hairy; on the anterior margins of all plates the hairs are fewer and rather rudimentary, while especially the inner and posterior margin of the two posterior pairs of plates is densely set with rather short hairs (omitted in Fig. 1 *a*). (The marsupium was empty.)

Abdomen. The segments are distinctly separated on the dorsal side. The five anterior segments, all comparatively broad, on each side produced as good-sized free plates, which mostly are cut off in a more or less oblique direction; on the left side all these pleural plates are bent obliquely upwards. The ventral side of these segments shows a similar but less regular division into low lamellæ as that of the posterior thoracic segments. The pleopods of medium size, each with two subequal rami, the basal part of which is thicker, somewhat fleshy, the distal part more lamellar; some of the rami are oblong-triangular and distally almost produced, others are distally broader and rounded; almost the whole, or at least the major basal part of the ventral surface of all rami is furnished with conspicuous rounded knots, some of which plainly show that this structure is a rudimentary ramification; the pleopods decrease somewhat in size from before backward. Each uropod (Fig. 1) is an oblong, glabrous lamella, which is as large as, or a little larger than, a ramus of the first pleopod.

Size. From the front to the apex of the longest uropod the specimen is 13 mm., and to the end of the last abdominal segment 11.2 mm.; it is 6.6 mm. broad.

b. *Male.*

The body is very elongate, about 3½ times longer than broad (Fig. 1*e* and 1*f*).

Head. It is completely fused with the first thoracic segment. The eyes are very small, light grayish, and scarcely visible when the animal is seen from above. The frontal part bends much downward and forms a high border, which covers the basal part of the antennulæ and the antennæ (Fig. 1*g*); the margin is rather slightly curved. The antennulæ tolerably short, 3-jointed; the basal joint longer and very much thicker than the second; the third joint very slender and rather short. The antennæ rather long, 8-jointed; the first joint a little longer and about twice as broad as the second, which is about as long as, and much thicker than, the third and especially the fourth; the four distal joints exceedingly small. The mouth conical and protruding, but it was utterly impossible to study its elements with any certainty without a dissection.

Thorax. The segments, when seen from above, with their lateral outline feebly rounded and the incisions between them short. Each segment with a median, rather high, basally very broad and distally rounded cone on the ventral side (Fig. 1*f*); this cone is smaller on the two first segments than on the others. A leg of the first pair is shown in Plate III. Figure 5, and the corresponding leg of the fifth pair in Figure 5*a*; the general shape and the armature of the fifth and the sixth joint — the first joint as usual fused with the thorax and consequently not drawn — are easily seen.

Abdomen. It occupies one third of the total length, and decreases posteriorly very little in breadth. The six segments are all well separated from each other. The five anterior segments with the lateral part almost triangular, when seen from above; each with a ventral cone as those in the thoracic segments, and, besides, each pleopod is developed as a protuberance of considerable size and directed obliquely inward and a little backward. The sixth segment relatively broad, on each side with a large, narrow conical, obtuse process, probably the uropod, originating from the side and directed somewhat outward and much backward; the posterior margin of the segment is angular.

Size. It is 4.1 mm. long to the apex of the uropods.

Habitat. The described pair were found in the branchial cavity of a specimen of *Nematocarcinus agassizii* Fax., from Station 3407 (Lat. 0° 4′ S., Long. 90° 24′ 30″ W.), 885 fathoms. The swelling of the carapace is oblong, and not very high.

11. Munidion princeps, n. gen., n. sp.

Plate IV. Fig. 2–2 *e*; Plate V. Fig. 1–1 *d*.

Two females with their males were secured.

a. *Female.*

The body, when seen from above (Fig. 1), of an almost pyriform outline, and not quite 1½ times longer than broad (the uropods not included). One specimen has the right margin convex, — a "right" specimen; the other is a "left" specimen.

Head. It is much broader than long and encircled posteriorly and on the major part of its sides of the first thoracic segment; the dorsal surface is somewhat convex, and the frontal border tolerably broad and bent conspicuously upward; the anterior margin is slightly convex. The antennulæ (Plate IV. Fig. 2) separated by a frontal plate; they are of medium size, 13-jointed; the basal joint is comparatively large, the third extremely small. The antennæ are rather short, 3-jointed; the basal joint is long and exceedingly broad, almost triangular, with the expanded inner border overlapping the outer part of the mandibles and the lateral angle of the labrum, the produced anterior angle extends to the frontal plate and the second joint is inserted on the vertex of the triangle; the last named joint is short and slender, the third joint exceedingly small. The frontal plate is broadly triangular with obtuse vertex, completely occupying the small space between the foot of the antennulæ, the anterior angle of the antennæ, and the labrum. The labrum (*c*) scarcely of medium size, somewhat broader than the hemi-cylindrical hypopharynx. Hypopharynx, mandibles (*d*), maxillulæ, and maxillæ need no special mention. The left maxilliped is shown in Figure 2 *a*; the most interesting character is that the palp has almost disappeared, as we see but a somewhat produced angle. The border behind the maxillipeds is very well developed, with a number of small protuberances, and having on each side two oblique slender processes, of which the inner is long, the outer very long.

Thorax. Ovarian bosses are developed on all segments; they are very prominent, most of them almost semi-globular (on the drawn specimens they are accidentally — caused by pressure — more or less depressed on the right side of the second to the fourth segment); in the three anterior segments they are large and gradually decrease in size backward, the two posterior pairs almost petiolated, the seventh pair small (in the small specimen the two posterior pairs are even reduced to prominent, distally not swelled processes). The bosses do not occupy the sub-lateral part of the segments to its whole length, only the larger posterior portion, yet not extending to the posterior margin. The pleural plates are comparatively large, oblong, rounded, thus occupying the whole or at least most of the lateral margin; in the posterior segments they are broader and overlap each other considerably; their convex ventral side with numerous small tubercles and oblong knots. The three posterior segments on the ventral side with an interrupted row of very short fleshy keels; the other segments are not examined. The legs are robust; the second joint (Fig. 1 *b* and 1 *d*) on the outer side with a very high expansion, shaped as an oblique plate, which is about as high as long and somewhat shorter than the length of the joint, on both sides with irregular small protuberances; the other joints normal. In Figure 1 *b* is shown the first left leg with the marsupial plate; this plate shows on the under side a deep transverse furrow and more forward a group of low knots, on the upper side (Fig. 1 *c*) a kind of transverse keel, the marginal portion of which is divided into numerous irregular, small, thin-skinned processes. The basal part of the other four pairs of plates with numerous knots (Fig. 1 *a*). (The marsupium of both specimens with eggs.)

Abdomen. The five anterior segments with very large rounded pleural lamellæ, the anterior of which are somewhat transverse, the posterior oblong; the lamellæ cover the main part of one another, a large portion of the dorsal surface of the anterior segments, and the whole dorsal surface of the posterior ones. In Figure 1 the fifth pair of lamellæ are lettered a^5. The second to the fifth segments on the ventral side each with a transverse row of short fleshy processes or knots, or lamellar keels; the first segment with an interrupted series of low lamellæ. The sixth segment (posteriorly behind the attachment of the uropods produced into an oblong, distally rounded and swelled, almost petiolated process. Each pair of pleopods consists of two large rami; in the anterior pairs these are shorter and rather broadly triangular, backwards they gradually become elongate. The uropods biramous, the rami similar to those of the last pleopods; in Figure 1 *a* the visible distal part of the rami on the left side of the figure are marked with 6, on the right side with 6^1. The main part, or almost the whole, of both surfaces of the pleural lamellæ and of the pleopods and uropods is set with very low and irregular minute keels and more rounded protuberances, which are most developed on the anterior pleopods.

Size. The largest specimen — which has been taken as type for all the figures — is 14.2 mm. long to the end of the abdomen, 17.3 mm. long to the apex of the longest ramus of the uropods, and 10.9 mm. broad. The other specimen measures 15.6 mm. to the end of the uropods.

b. *Male.*

One specimen (Plate IV. Fig. 2 *b*) is symmetrical and undoubtedly normal; the other specimen (Fig. 2 *c*) is anomalous, not symmetrical, and somewhat misshapen, — especially the abdomen is conspicuously different. In the following the normal specimen is described, with some remarks concerning the other.

The body is considerably depressed and relatively broad, scarcely 2½ times longer than broad.

Head. Its dorsal surface almost flat, with irregular rugosities. The eyes are very small and dark. The frontal part bends feebly downwards; the anterior margin is considerably curved. The antennulæ (Plate IV. Fig. 2 *d*) are rather long, 3-jointed; the basal joint thick, the second longer than the first and comparatively thick, the third rather short and slender. The antennæ of medium length, 3-jointed; the basal joint of medium length and almost twice as broad as long, with the outer margin concave; the second joint is attached to the anterior half of the outer margin of the first joint; it is stout and twice as long as the basal one; the third joint is rather short and slender. The labrum of medium size, with the anterior margin very convex; its median part is covered by the hypopharynx, which extends forward to the middle of the basal joint of the antennulæ. The hypopharynx is long, not broad, and tapers somewhat towards the rounded apex. The mandibles and the maxillulæ are easily seen in the figure; a rounded protuberance behind each maxillula most probably represents the maxilla; maxillipeds I have not been able to discover.

Thorax. The fifth segment is the broadest, and from that the thorax decreases a little in breadth towards both ends. The segments, when seen from above, with the lateral outline much rounded, but the incisions between them are short. On the ventral side a median, very conspicuous cone on each segment. The legs subequal in structure; all are relatively short and very thick, but the fourth and fifth pairs are somewhat larger and still more clumsy than the first pair; Figure 2 *e* (on Plate IV.) represents the left leg of the first pair, and a description is scarcely needed.

Abdomen. It does not occupy one third of the length of the body, and anteriorly it is somewhat narrower than the last thoracic segment; it is triangular with rounded angles, a little longer than broad, and the lateral outline is somewhat sinuous, which shape indicates the segmentation. All segments are completely fused; vestiges of transverse sutures are scarcely discernible on the dorsal, but rather distinct on the ventral side.

Size. The specimen is 3.3 mm. long.

The misshaped male is exhibited in Figure 2 *c* (on Plate IV.). The outline of the thorax is somewhat irregular; the abdomen is very wry, with all the segments well separated on the dorsal surface, and the last segment having about the shape of an oblique square. The result of this deformity is, in my opinion, very interesting.

Habitat. The label states that the two females (with their males) were found in the branchial cavity of *Munida refulgens* Fax., from Station 3378 (Lat. 3° 58′ 20″ N., Long. 81° 36′ W.), 112 fathoms.

12. **Pseudione galacanthæ**, n. sp.

Plate V. Fig. 2–2 *i*.

Five adult females and the same number of males have been transmitted. (Compare "Habitat.")

a. *Female.*

The body about 1½ times longer than broad.

Head. It is somewhat broader than long, fused with the considerably curved first thoracic segment and encircled forward to the antero-lateral angle, while its anterior margin is slightly curved; the frontal border is rather narrow and turned somewhat upwards; the dorsal surface is slightly convex. The antennulæ (Fig. 2 *b*, *a*) are in contact anteriorly, posteriorly they are separated by a small, triangular frontal plate (*p*); they are of about medium size, 3-jointed; the basal joint is rather large, thick, the second shorter and more slender, the third very small, terminating in an exceedingly short bristle. The antennæ (*b*) are 4-jointed, rather short; the basal joint is very large, forming almost an oblique oval, yet the inner margin is almost straight, the outer very convex, and the second joint originates from its extero-anterior angle; the second and third joints are short and slender, the fourth very small, terminating in an exceedingly short bristle. The frontal plate is already mentioned. The labrum is very broad; the hypopharynx is oblong-triangular with rounded vertex. Mandibles (*d*), maxillulæ (*e*), and maxillæ (*f*) do not present any interesting peculiarities. The left maxilliped is shown in Figure 2 *c*; the palp is very conspicuous, with some hairs, but not jointed. The border behind the maxillipeds is well developed, with numerous small, irregular protuberances, and only one pair of processes which are long and distally narrow.

Thorax. The four anterior segments with ovarian bosses, which are low, and occupy about two thirds of the lateral margin of each segment; the pleural plates which occupy the remaining one third of the margin, are short or narrow. The three posterior segments without bosses, but the pleural plates occupy the entire margin and are developed as lamellæ, increasing gradually in length and turning more backward from the fifth to the seventh segment; besides they are longer on the convex than on the other side of the animal. The legs are rather stout (Fig. 2 *d* and Fig. 2 *e*); the second joint about as broad as long, owing to the fact that on the whole outer side it is much expanded, with the outline almost semicircular; the fourth joint with a keel on the inner margin, and two short, knot-like keels are found on the same margin of the posterior, but disappear on the anterior pairs of legs. The first left leg, with its marsupial plate, is shown in Fig. 2 *d*; the plate has on the lower side a broad and high transverse keel, and on the upper side a structure similar to that in Munidion (see above). Only the last segment on the ventral side with numerous small incisions and between these low fleshy projections; this structure is found both at the anterior and the posterior margin of the segment.

Abdomen. It occupies less than one third of the length of the animal, and the segments are well separated on the dorsal surface. The pleural plates are very large and lamellar, partly overlapping one another, in the first segment somewhat longer than those of the last thoracic segment, and then gradually increasing in length and turning more backward from the first to the fifth segment. The ventral side of the five anterior segments about as in the preceding species. Each pleopod with two triangular or ovate rami of medium size; the pleopods decrease somewhat in size from before backward, and the outer ramus is as a rule a little smaller than the inner one. Each uropod consists of one ramus (Fig. 2 *b*) which is oblong-ovate and considerably smaller than the pleural plates of the fifth abdominal segment.

Size. The largest specimen is 10.4 mm. long to the apex of the sixth abdominal segment, 11.8 mm. to the end of the uropods, and 7.4 mm. broad. The smallest specimen — with eggs in the marsupium — is only 7 mm. long to the end of the abdomen, and 5.8 mm. broad.

b. *Male.*

The body is very elongate (Fig. 2 *f*), between $3\frac{1}{2}$ and 4 times longer than broad.

Head. The dorsal surface is convex, the antero-lateral margin much curved, and the anterior part of the head bends somewhat downward. Eyes could not be detected, but we find small frontal impressions, which vary very much in different specimens (in one specimen two pairs were found). The antennulæ (Fig. 2 *g*) of medium length, 3-jointed; the basal joint thick and almost globular, the second shorter and much narrower than the first, the third minute. The antennæ of medium length, 5-jointed; the first joint thick and almost globular; the three following joints gradually a little shorter and much narrower; the apical joint minute. The labrum extremely broad, crescent-shaped. The hypopharynx reaches to the middle of the labrum; it is rather long, of medium breadth, tapering somewhat towards the rounded end. Mandibles, maxillulæ, and maxillæ (*f*) normal; the maxilliped (*g*) has the shape of a rather small oblong triangle.

Thorax. The fifth segment is the broadest, a little broader than the seventh, and considerably broader than the first segment. The lateral outline of the segments either rounded or (Fig. 2 *f*) more straight with rounded angles; the incisions between the segments narrow, triangular, and very deep. The ventral surface without conical protuberances. The legs more slender than in the preceding form; from before backward to the fifth pair they increase a little in length and their hand in size, and from the fifth to the last pair at least the hand decreases somewhat in size. In Figure 2 *h* is shown the left leg of the first pair, and in Figure 2 *i* that of the seventh pair.

Abdomen. It occupies about two fifths of the total length of the animal, and decreases in breadth from before backward to the small square sixth segment. All segments are very movable; seen from above, their lateral portion in the large specimen is triangular with the lateral angles more or less acute, in the small specimens less triangular and rounded laterally. In the anterior segments rudiments of pleopods are either scarcely discernible or visible as very low and broad rounded eminences.

Size. The largest specimen (Fig. 2 *f*) is 4.8 mm. long; a smaller specimen from which the three analytical figures have been drawn, is 3.5 mm. long; a small specimen is only 2.9 mm. long.

Habitat. The label indicates that the five adult females (with their males) were found in the branchial cavity of *Galacantha diomedeæ* var. *parvispina* Fax., from Station 3435 (Lat. 26° 48′ 0″ N., Long. 110° 45′ 20″ W.), 859 fathoms. In the Report on the Stalk-eyed Crustacea of the "Albatross" Expedition of 1891, W. Faxon writes (p. 81): "Seven specimens (5 males, 2 females) of var. *parvispina* house a Bopyrus in the left branchial chamber."

13. **Parargeia ornata,** n. gen., n. sp.

Plate VI. Fig. 1–1 *i*.

Only one female and its male are found.

a. *Female.*

The body is much distorted and scarcely $1\frac{1}{5}$ times longer than broad.

Head. It is comparatively very broad, but otherwise of the same shape as in *Munidion* (*ante*, p. 115). The antennulæ (Fig. 1 *b*) separated by a frontal plate (*p*), of medium size, 3-jointed; the basal joint comparatively long and thick, the second short and narrow, the third exceedingly small. The antennæ (*b*) similar in shape to those of Pseudione (see above), but larger and 6-jointed; the basal joint very large, forming about an oblong oval, with both margins a little convex; the second joint is attached at the antero-exterior angle of the first, and is tolerably short and slender, yet longer and considerably thicker than the third; the three distal joints are exceedingly small. The frontal plate (*p*) rather large, about three times broader than long, anteriorly emarginate. The labrum exceedingly large, in the middle very short, but on each side forming a large oblique plate (*c*) which overlaps the distal part of the mandible and the maxillula, and the lateral part of the hypopharynx. This organ (*h*) is triangular and broader towards its base than in the preceding forms. The mandibles (*d*) extend in the middle with their acute tip beyond the end of the hypopharynx. Maxillulæ (*e*) and maxillæ (*f*) need no mention. The left maxilliped is shown in Figure 1 *c*; the palp consists of a prominent basal part and a small terminal joint. The border behind the maxillipeds well developed, with two pairs of long, oblique, distally slender processes.

Thorax. Ovarian bosses are found on the four anterior segments; they are oblong, considerably convex, and occupy from less to more than half of the sub-lateral portion of each segment. By a conspicuous or even deep furrow they are set off from the anterior part of the pleural plates, which lie outside or more beneath the bosses, are much arched, and look almost like "epimera" in

Cymothoidæ. The posterior portion of the lateral part of the segments mentioned is more or less protruding, rounded or angular, and must be considered as the posterior division of the pleural plate (compare *Cryptione*). On the three posterior segments the pleural plates are deeply incised, divided into a larger, broader, and more produced anterior part, and a much smaller, narrower, and less produced posterior one, which is more or less obsolete on the last segment. At least on the posterior segments the ventral side shows the usual low fleshy keels. The legs are slender; the second joint proximally on the outer side with a considerable rounded expansion, which is comparatively longer and broader on the anterior (Fig. 1 *d*) than on the posterior (Fig. 1 *e*) pairs; the other joints are normal. In Figure 1 *d* is shown the first leg with its unusually large marsupial plate; the transverse furrow is not deep; on the upper side the keel is tolerably high and much compressed, but without marginal processes. The marsupial plates do not quite reach each other at the middle; their natural position was somewhat disturbed in the specimen, and therefore it was necessary to make use of construction in Figure 1 *a*.

Abdomen. The segments distinctly separated at the middle on the flat dorsal surface. No pleural plates. The segments fleshy on the ventral side; only the first segment with slight furrows. The pleopods very curious, and rather similar to each other; each consists of two rami; the outer ramus is a very long, subrectangular or distally rounded, somewhat fleshy lamella, which is placed at the margin of the segment; the inner ramus is proportionally short, more or less ovate, fleshy, originating at some distance from the outer ramus, and on the left side of the animal it conveys the impression that the basal half is fused with the ventral side of the segment. (I am aware that another interpretation of the described facts could be advanced, namely, that the outer ramus is a pleural plate set off by a kind of articulation, and that the inner ramus in reality represents the entire pleopod, but this opinion I cannot share.) Each uropod consists of a single lamella of about the same shape and size as the nearest outer ramus of a pleopod.

Size. The specimen is 8.5 mm. long to the apex of the abdomen, 10.3 mm. long to the end of the uropods, and 7.2 mm. broad.

b. *Male.*

The shape of the body is interesting. It increases uniformly but rather slightly in breadth from the head to the last thoracic segment, and the abdomen is anteriorly somewhat broader than the preceding segment, triangular with rounded angles, somewhat broader than long, the anterior margin a little concave and the lateral margins convex. The body is a little more than 2½ times longer than the width of the abdomen.

Head. The dorsal surface is convex, the median part of the anterior outline almost straight. A pair of small spots or minute depressions perhaps represent the eyes. When the head is seen from below (Fig. 1 *g*), it is observed that the frontal border arises like a broad and rather high transverse keel above the attachment of antennulæ and antennæ. The antennulæ of medium length, 3-jointed; the basal joint thick, the second shorter and much narrower than the first, the third short and very slender. The antennæ rather short, 7-jointed; the first joint very thick, the second of about the same length but somewhat more slender, the third somewhat shorter and more slender than the second, the fourth rather short and very slender; the three distal joints exceedingly small. The mouth forms a basally broad, somewhat protruding oblique cone, but without a dissection I was not able to recognize several of the parts with any certainty; the figure will show what I believed I saw.

Thorax. The segments much arched on the dorsal side, the incisions between them of medium length, and most of them very narrow; their lateral margin is, when seen from the side, much more rounded than if seen from above. No ventral cones. The legs increase somewhat in length from before backward, but at the same time their hand decreases in size from the first (Fig. 1 *h*) to the seventh (Fig. 1 *i*) pair, and besides alters conspicuously in shape.

Abdomen. It occupies somewhat more than one fourth of the length of the animal; its outline is described above. All segments are completely fused, so that only some transverse, partly very indistinct furrows, but no sutures, are found on the dorsal surface. About half way between the median line and the lateral margin the dorsal surface presents a broad longitudinal depression, and in the median line a little behind the anterior margin a prominent knot. The ventral surface does not seem to be quite normal, but the following characters certainly are of importance: no rudiments of pleopods are to be discovered, but in the median line are found three protuberances: the first small, the second rather large, the third shaped as a short transverse keel.

Size. The specimen is 4.1 mm. long.

Habitat. In the branchial cavity of *Sclerocrangon procax* Fax., from Station 3418 (Lat. 16° 33′ N., Long. 99° 52′ 30″ W.), 660 fathoms, 1 female with a male.

14. **Bathygyge grandis**, n. gen., n. sp.

Plate VI. Fig. 2–2 *c*.

Only a male, and the posterior part of a female have been sent to me.

a. *Female.*

The rudiment consists of the posterior part of the thorax, bearing three legs on one and two on the other side, and the abdomen.

Thorax. The pleural plates are very large oval lamellæ, only connected with the segment by somewhat less than the posterior half of their interior margin, and this result is due to the fact that they anteriorly are very much produced, highly overlapping each other, and posteriorly rather shortly produced. The legs are tolerably slender; the second joint not expanded; the fifth joint elongate, in the last pair as long as the hand.

Abdomen. It is turned to the left in a startling degree, and is proportionally small, — perhaps very small. The dorsal surface is soft-skinned, the segments more or less distinctly separated. Pleural plates not developed. The pleopods quite soft, of medium size, decreasing conspicuously in size from before backward and attached to the lateral margin; each pleopod consists of a short peduncle and two lamellar oblong rami; the outer ramus much larger than the inner one. The uropods biramous; the outer ramus a little smaller than the outer of the fifth pleopod, the inner ramus very short, almost rudimentary. The pleopods are curled to such a degree that it would have been impossible without much construction to draw a sketch of the abdomen.

b. *Male.*

The body is a little more than three times longer than broad, and from the fourth thoracic segment it decreases in breadth towards both ends (Fig. 2).

Head. The dorsal surface rather convex; the median portion of the anterior margin almost straight. No eyes. The frontal border bent slightly downwards (Fig. 2 *a*). The antennulæ rather short, 3-jointed; the basal joint tolerably thick, and partly overlapped by the rostrum; the second joint slender and rather short, the third very small. The antennæ comparatively long, 7-jointed; the four proximal joints of about the same length, but decreasing much in breadth from the rather thick basal joint to the fourth one; the fifth joint is short and very slender, the two last joints exceedingly small. The mouth forms a rostrum which, when seen from below, is triangular, considerably depressed and directed forward, reaching almost to the frontal margin of the head. The hypopharynx is very large, and just outside it is seen the very oblong lateral part of the labrum (*d*), the median part of which is concealed by the hypopharynx; at first I believed that these oblong organs were the mandibles, but a closer examination gave the result mentioned, while the mandibles, being needles with brown apex, were discovered within the rostrum. Maxillulæ are not observed; the maxillæ (*f*) are small semicircular lobes lying considerably behind the posterior edge of the labrum. The maxillipeds (*g*) are short, extremely slender, almost styliform.

Thorax. The segments are rather convex, the incisions between them comparatively broad and very deep; the lateral margins are much curved when seen from the side. The legs increase considerably in length, and very much in thickness, from the first (Fig. 2 *b*) to the fifth pair (Fig. 2 *c*) which is robust, with the hand very large; the two posterior pairs again decrease somewhat in size. The terminal margin of the hand is deeply concave, thus differing considerably from the preceding forms.

Abdomen. It occupies scarcely one fourth of the length of the animal; it is narrower than the last thoracic segment, shortly ovate in outline, without the slightest rudiment of segmentation or abdominal feet; both the ventral and especially the dorsal surface are very convex.

Size. Uncommonly large, being 7 mm. long, and 2.3 mm. broad.

Habitat. The branchial cavity of *Glyphocrangon spinulosa* Fax., from Station 3424 (Lat. 21° 15′ N., Long. 106° 23′ W.), 676 fathoms, 1 female with its male.

Remarks. The species is established essentially on the very large male, the mouth parts of which are very different from those of other forms known to me. I hope that it will prove to be rather easy to recognize the form, but I hesitated to establish the new genus, the knowledge of the female being very incomplete. However, I found it impossible to refer the species to any of the genera hitherto published.

ONISCIDÆ.

15. Porcellio lævis Latr. (1804).

I will only refer to the account in G. Budde-Lund's Crustacea Isopoda Terrestria, 1885, which is the principal work on the Oniscidæ; the author (pp. 138–140) describes the species, presents an enormous quantity of synonymy and references to earlier authors, and adds a very long list of localities for this almost cosmopolitan form.

Habitat. Chatham Island, Galapagos (March 29, 1891), four specimens (determined by G. Budde-Lund).

Zoölogical Museum, Copenhagen,
September 16, 1897.

EXPLANATION OF THE PLATES.

PLATE I.

1. *Eurycope pulchra*, n. sp.

Fig. 1. Female seen from above, × $\frac{9}{4}$. Of the antennulæ only the two proximal joints, of the antennæ only the four proximal joints are drawn; the thoracic legs omitted, with the exception of the basal joint of the four anterior pairs.

Fig. 1 *a*. Female seen from left side, × $\frac{9}{4}$. Antennulæ and antennæ as in the preceding figure; the first thoracic leg is drawn, but of the six other pairs only the basal and the major part of the second joint are shown.

Fig. 1 *b*. Right mandible seen from below, × 11.

Fig. 1 *c*. Left mandible seen from below, × 11; most of the palp omitted; *a*, cutting portion; *b*, molar process; *l*, lacinia mobilis; *m*, muscle (only the basal part); *p*, palp (proximal part).

Fig. 1 *d*. Left maxillula seen from below, × 11; 1, first joint; l^1, lobe of the first joint; 2, second joint; 3, third joint; l^3, lobe of the third joint.

Fig. 1 *e*. Left maxilla seen from below, × 11; 1, first joint; 2, second joint; l^2 lobe of the second joint; 3, third joint; l^3, lobes of the third joint.

Fig. 1 *f*. Left maxilliped seen from below, × 11; 1, first joint, *ep.* its epipod; 2, second joint; *h*, its coupling hooks; l^2, lobe of the second joint; 7, seventh joint.

Fig. 1 *g*. First thoracic leg, × $\frac{9}{2}$.

Fig. 1 *h*. Thoracic leg of fifth pair, × $\frac{9}{2}$; the natatory hairs omitted; 1, first joint; 2, second joint; 7, seventh joint. This and the preceding analytical figures are drawn from parts of a female.

Fig. 1 *i*. Abdomen of a male seen from below, × $\frac{11}{3}$; *a*, pleopod of first pair; *b*, pleopod of second pair; *c*, uropod; *d*, anal doors.

2. *Eurycope scabra*, n. sp.

Fig. 2. Female seen from above, × 2. The antennulæ completely wanting; of the antennæ the four proximal joints, and of the thoracic legs only the basal joint are seen. As to the correctness of the outline of thorax and abdomen, see the description.

Fig. 2 *a*. Left mandible seen from below, × $\frac{25}{2}$.

Fig. 2 *b*. Left maxillula seen from below, × $\frac{25}{2}$.

Fig. 2 *c*. Left maxilla seen from below, × $\frac{25}{2}$.

Fig. 2 *d*. Left maxilliped seen from below, × $\frac{25}{2}$.

PLATE II.

1. *Eurycope scabra*, n. sp. (continued).

Fig. 1. First thoracic leg of female seen from the exterior side, × 6.

2. *Æga maxima*, n. sp.

Fig. 2. Female without marsupium, natural size; the apex of the last abdominal segment was wanting.

Fig. 2 *a*. Right side of thorax of the same specimen showing the "epimera," etc., natural size.

Fig. 2 *b*. Left leg of the second pair of the same specimen seen from below, scarcely × 3.

Fig. 2 *c*. Left leg of the fifth pair seen from below, scarcely × 3.

3. *Æga acuminata*, n. sp.

Fig. 3. Head of female without marsupium, seen half from above and half from in front, × 3.

Fig. 3 *a*. Right side of thorax and of the two anterior abdominal segments of the same specimen, × 2.

Fig. 3 *b*. Posterior part of abdomen with the uropods of the same specimen, scarcely × 3.

4. *Æga plebeia*, n. sp.

Fig. 4. Head and first thoracic segment of a good-sized female without marsupium, seen half from above and half from in front, × $\frac{8}{3}$.

Fig. 4 *a*. Right side of thorax and of the two anterior abdominal segments of the same specimen, × $\frac{7}{3}$.

Fig. 4 *b*. Left leg of second pair of the same specimen, seen from below, × $\frac{9}{2}$.

Fig. 4 *c*. Left leg of fifth pair of the same specimen, seen from below, × $\frac{9}{2}$.

Fig. 4 *d*. Posterior part of the abdomen with the uropods of the same specimen, × $\frac{8}{3}$. The hairs and spines on the uropods and on the posterior margin of the last abdominal segment omitted.

5. *Æga longicornis*, n. sp.

Fig. 5. Female without marsupium, × about $\frac{8}{3}$.

Fig. 5 *a*. Right side of thorax and of the two anterior abdominal segments of the same specimen, × $\frac{9}{2}$.

Fig. 5 *b*. Posterior part of abdomen with the uropods of the same specimen, ×$\frac{11}{2}$.

PLATE III.

1. *Æga longicornis*, n. sp. (continued).

Fig. 1. Left leg of second pair of the female exhibited in the preceding plate, seen from below, × $\frac{13}{2}$.

Fig. 1 *a*. Left leg of fifth pair of the same female, seen from below, × $\frac{13}{2}$.

2. *Rocinela laticauda*, n. sp.

Fig. 2. Male (the largest specimen), natural size.
Fig. 2 *a*. Head of female without marsupium, seen from below, × 5.
Fig. 2 *b*. Right side of thorax of the small immature female, scarcely × 3.
Fig. 2 *c*. Left leg of second pair of the larger immature female, seen from below, scarcely × 4.
Fig. 2 *d*. Left leg of fifth pair of the same female, seen from below, scarcely × 4.
Fig. 2 *e*. Last thoracic segment and abdomen of the small immature female, scarcely × 3.

3. *Rocinela modesta*, n. sp.

Fig. 3. Head of female with marsupium, seen from below, × 6; the flagella of the antennæ are broken off.
Fig. 3 *a*. Left leg of second pair of the same female, seen from below, × $\frac{19}{3}$.
Fig. 3 *b*. Left leg of fifth pair of the same female, seen from below, × $\frac{19}{3}$.
Fig. 3 *c*. Last thoracic segment and abdomen of the same female, × 3.

4. *Irona foveolata*, n. sp.

Fig. 4. Female with marsupium, × $\frac{7}{3}$.
Fig. 4 *a*. Leg of second pair of "pullus stadii primi," × 22.
Fig. 4 *b*. Posterior part of abdomen of "pullus stadii primi," × 22.

5. *Cryptione elongata*, n. gen., n. sp.

Fig. 5. Leg of first pair of the male, × 111.
Fig. 5 *a*. Leg of fifth pair of the male, × 111.

PLATE IV.

1. *Cryptione elongata*, n. gen., n. sp. (continued).

Fig. 1. Female seen from above, × $\frac{13}{3}$.
Fig. 1 *a*. Same female seen from below, × $\frac{13}{3}$; *m.* male; *mxp.* maxilliped; 1′, rami of first pleopod on the left side (of the animal = right side of the figure); 2, rami of second pleopod on the right side; 4′, rami of fourth pleopod on the left side; 5, rami of fifth pleopod on the right side; 5′, rami of fifth pleopod on the left side; 6, uropods. The marginal hairs on the marsupial plates are omitted.
Fig. 1 *b*. Head of the female seen from below and both maxillipeds omitted, × 9; *a*, antennula; *b*, antenna; *c*, labrum; *d*, mandible; *e*, maxillula; *f*, maxilla; *g*, place of attachment of the maxilliped; *h*, hypopharynx; *l*, lobes or processes from the border behind the maxillipeds.
Fig. 1 *c*. Left maxilliped of the same female seen from below, × $\frac{19}{2}$; 1, first joint with its posterior expansion; 2, second joint; d^2, dilatation on the outer side of the second joint; *p*, palp.
Fig. 1 *d*. Left leg of first pair with its marsupial plate seen from below, × $\frac{19}{2}$; 2, second joint of the leg (the first joint being fused with the thorax).

Fig. 1 *e*. Male seen from above, $\times \frac{19}{2}$.

Fig. 1 *f*. Same male seen from below, $\times \frac{25}{2}$.

Fig. 1 *g*. Head of the same male seen from below, × 36.

2. *Munidion princeps*, n. gen., n. sp.

Fig. 2. Anterior part of the head of the large female seen from below, scarcely × 10; *c*, labrum; *d*, mandible; *f*, maxilla.

Fig. 2 *a*. Left maxilliped of the large female, seen from below, scarcely × 7.

Fig. 2 *b*. Normal male, $\times \frac{23}{2}$.

Fig. 2 *c*. Misshaped male, $\times \frac{23}{2}$.

Fig. 2 *d*. Head of the normal male, seen from below, × 39.

Fig. 2 *e*. Left leg of first pair of the normal male, × 44.

PLATE V.

1. *Munidion princeps*, n. gen., n. sp. (continued).

Fig. 1. The large female seen from above, about $\times \frac{16}{5}$; a^5, pleural plates of the fifth abdominal segment.

Fig. 1 *a*. Same female seen from below, about $\times \frac{16}{5}$; 1, rami of first pleopod on the right side (of the animal, left side of the figure); 1′, rami of first pleopod on the left side; 4, rami of fourth pleopod on the right side; 5, rami of fifth pleopod on the right side; 5′, rami of fifth pleopod on the left side; 6, rami of the right uropod; 6′, rami of the left uropod.

Fig. 1 *b*. Left leg of first pair with its marsupial plate of the same female, seen from below, scarcely × 7.

Fig. 1 *c*. Posterior part of the marsupial plate exhibited in the preceding figure, and seen from above, $\times \frac{19}{2}$.

Fig. 1 *d*. Left leg of sixth pair of the same female, scarcely × 7.

2. *Pseudione galacanthæ*, n. sp.

Fig. 2. Large female, seen from above, $\times \frac{9}{2}$; 6, uropods.

Fig. 2 *a*. Same female seen from below, $\times \frac{9}{2}$; 1′, rami of first pleopod on the left side (of the animal); 4′, rami of fourth pleopod on the left side; 5, rami of fifth pleopod on the right side; 5′, rami of fifth pleopod on the left side; a^5, pleural plates of fifth abdominal segment.

Fig. 2 *b*. Anterior part of the head of female, seen from below, × 10; *a*, antennula; *b*, antenna; *c*, labrum; *d*, mandible; *e*, maxillula; *f*, maxilla; *p*, frontal plate.

Fig. 2 *c*. Left maxilliped of female, seen from below, × 10.

Fig. 2 *d*. Left leg of first pair with its marsupial plate, seen from below, × 10.

Fig. 2 *e*. Left leg of sixth pair of female, × 10.

Fig. 2 *f*. Largest male, × 10.

Fig. 2 *g*. Head and a part of the first thoracic segment of a smaller male seen from below, × 39; *f*, maxilla; *g*, maxilliped.

Fig. 2 *h*. Left leg of first pair of the last named male, × 47.

Fig. 2 *i*. Left leg of seventh pair of the same male, × 47.

PLATE VI.

1. *Parargeia ornata,* n. gen., n. sp.

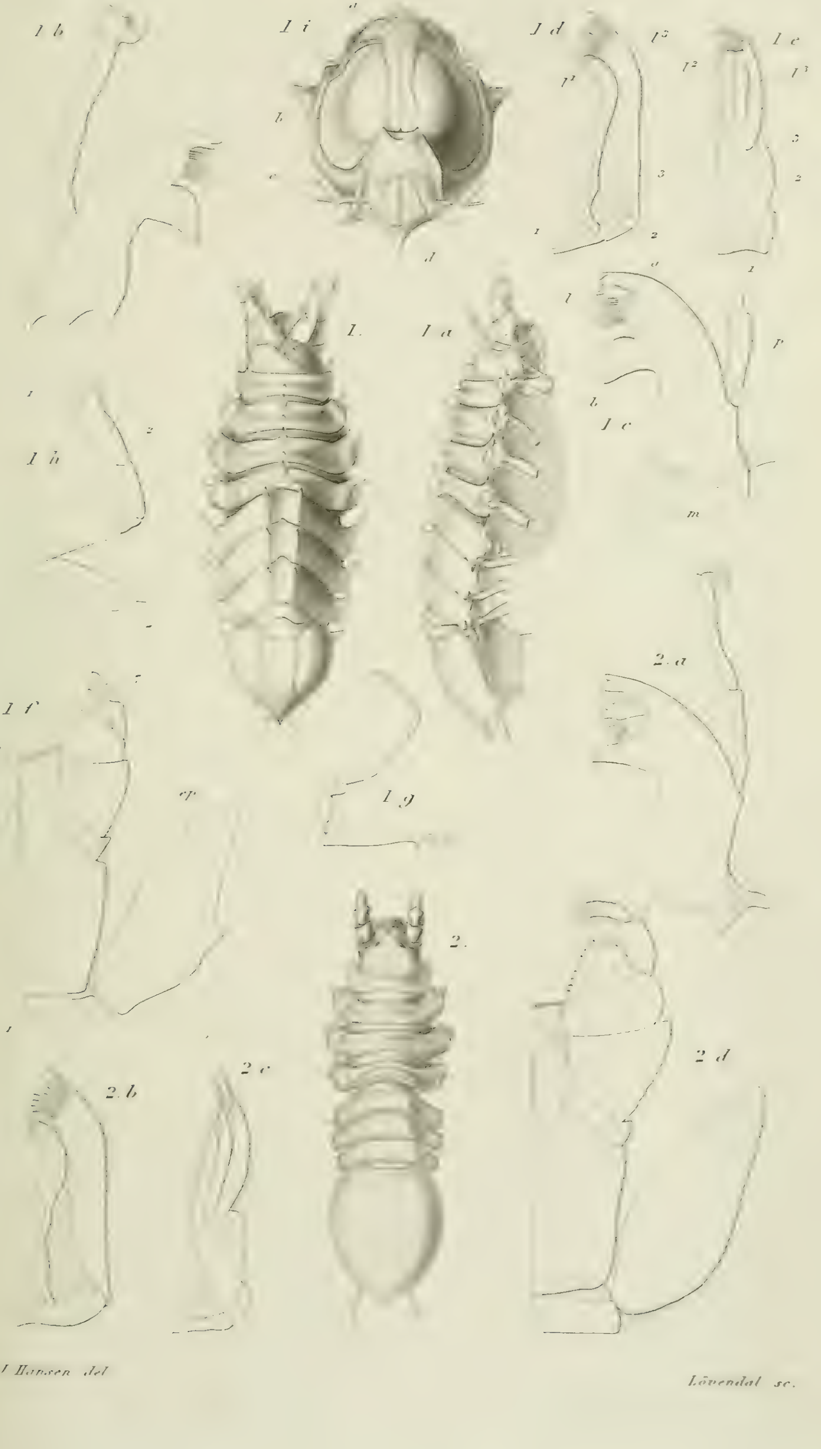
Fig. 1. Female seen from above, about $\times \frac{9}{2}$.
Fig. 1 *a*. Same female seen from below, about $\times \frac{9}{2}$; as to the marsupial plates see the description of the species.
Fig. 1 *b*. Anterior part of the head of the same female seen from below, × 13; *b*, antenna; *c*, labrum; *d*, mandible; *e*, maxillula; *f*, maxilla; *h*, hypopharynx; *p*, frontal plate.
Fig. 1 *c*. Left maxilliped of the same female seen from below, scarcely × 10.
Fig. 1 *d*. Left leg of first pair with its marsupial plate seen from below, scarcely × 10.
Fig. 1 *e*. Left leg of seventh pair of the same female, scarcely × 10.
Fig. 1 *f*. Male, $\times \frac{29}{3}$.
Fig. 1 *g*. Head of the same male seen from below, × 39.
Fig. 1 *h*. Left leg of first pair of the same male, × 46.
Fig. 1 *i*. Left leg of seventh pair of the same male, × 46.

2. *Bathygyge grandis,* n. sp.

Fig. 2. Male, scarcely $\times \frac{13}{2}$.
Fig. 2 *a*. Head of the male seen from below, × 26; *d* (by error instead of *c*), labrum; *f*, maxilla; *g*, maxilliped.
Fig. 2 *b*. Left leg of first pair of the male, × 19.
Fig. 2 *c*. Left leg of fifth pair of the male, × 19.

PLATE VII.

ROUTE OF THE "ALBATROSS."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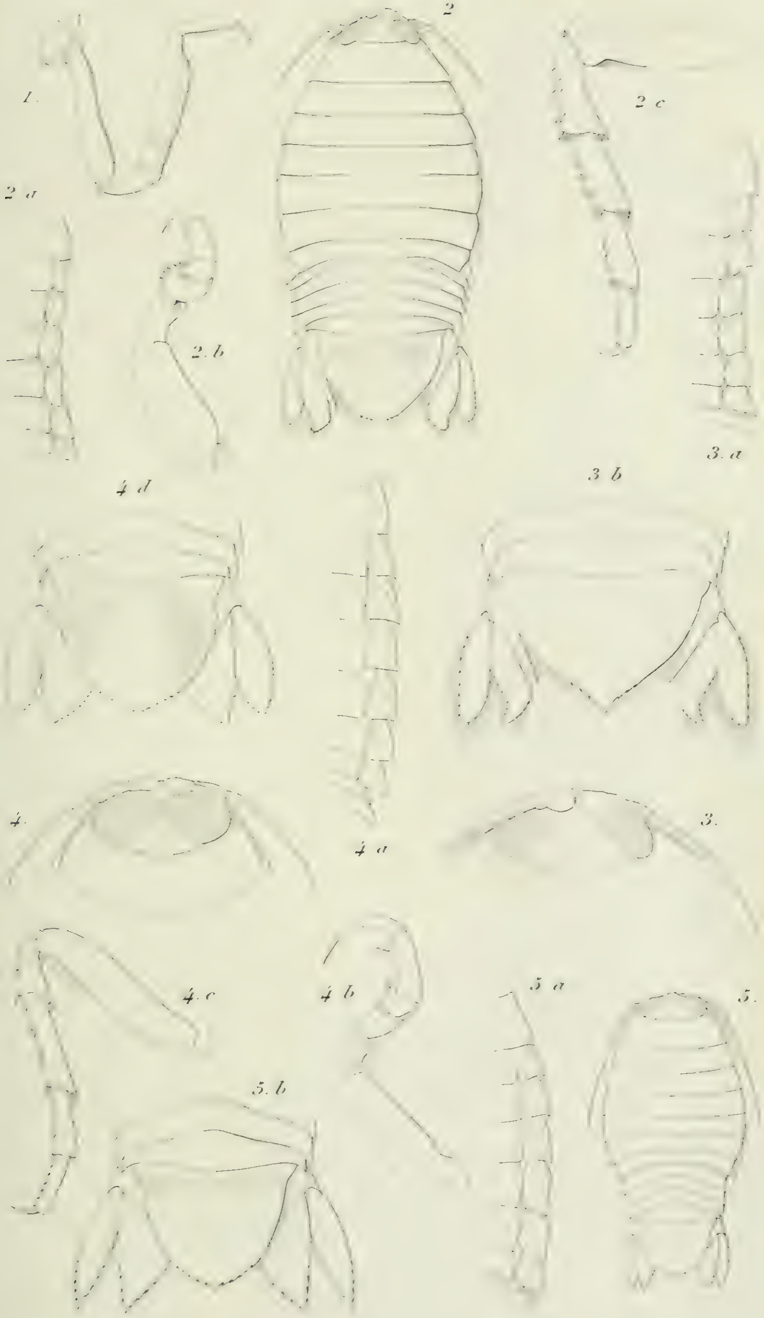
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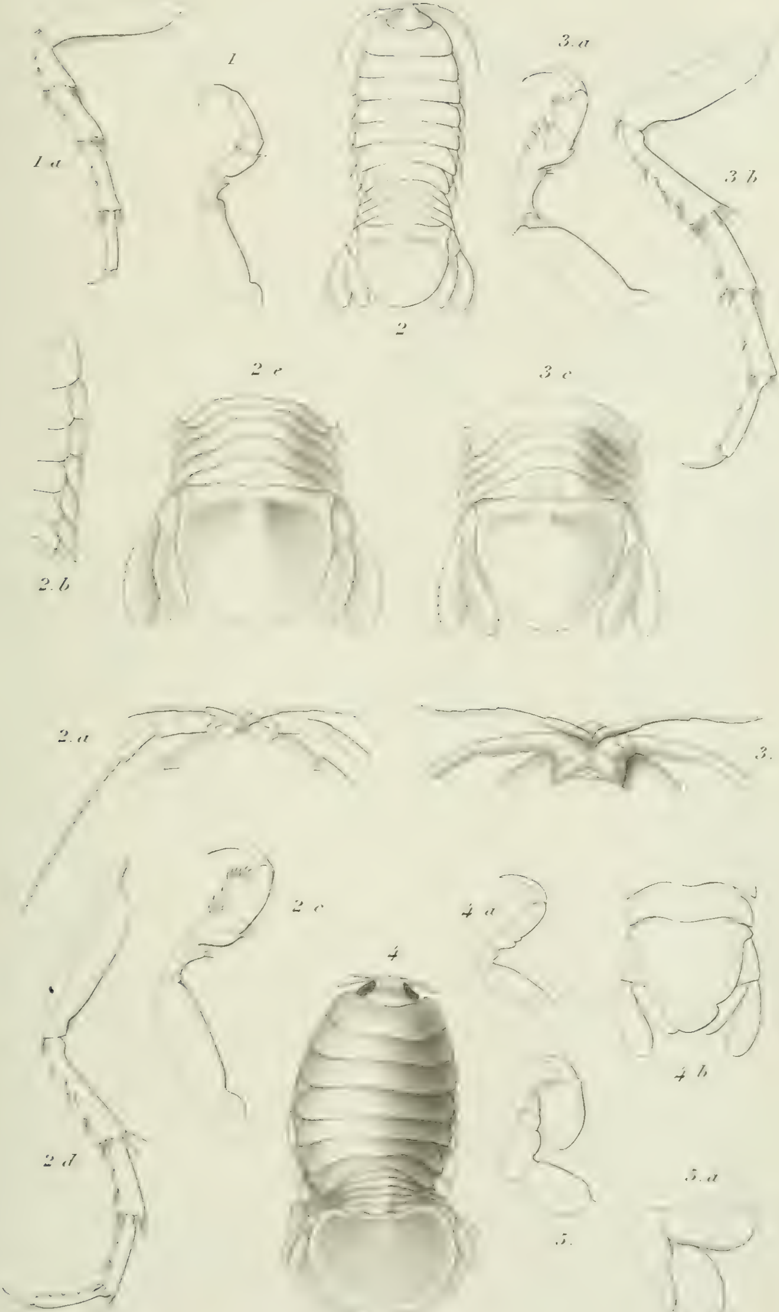
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Lövendal sc.

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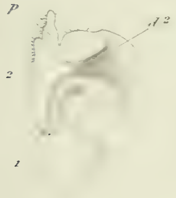

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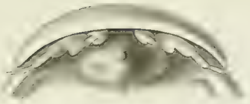

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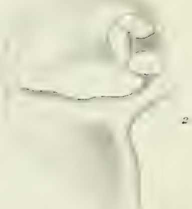

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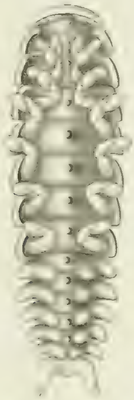

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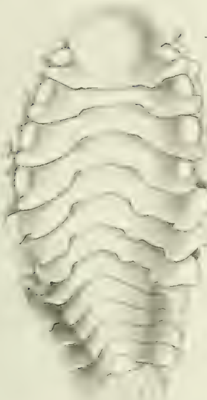

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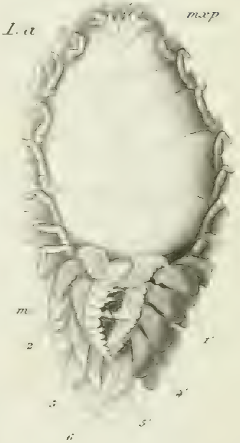
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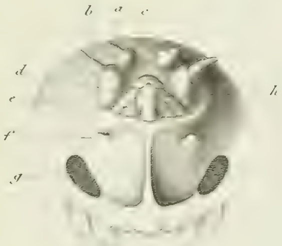

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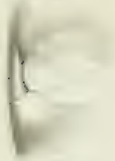
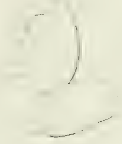


2 c

2 e



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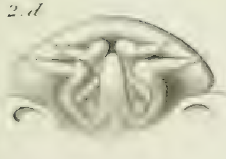

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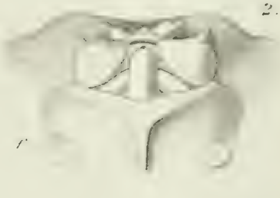

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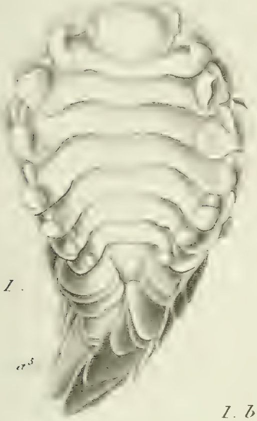
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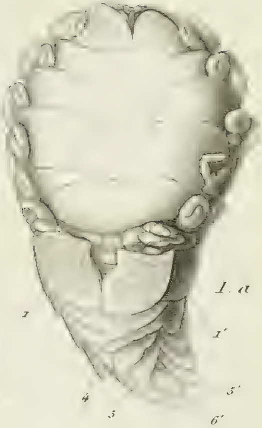
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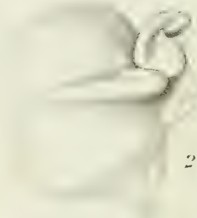
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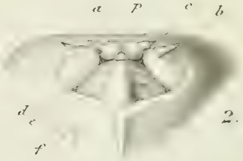
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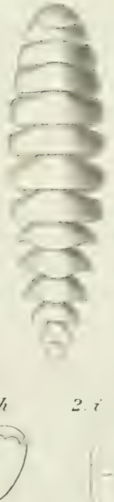
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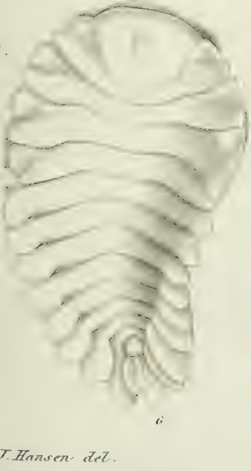
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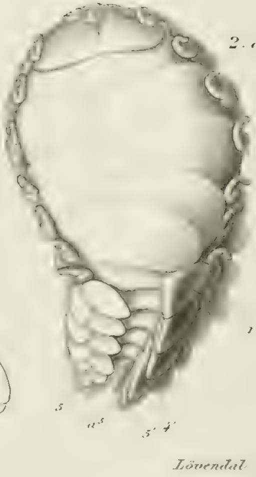
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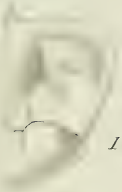
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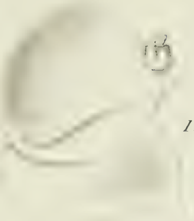
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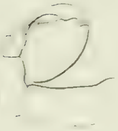
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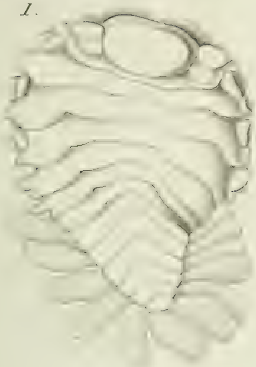

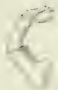
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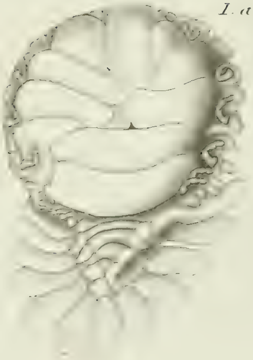

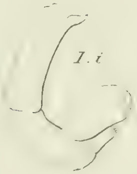
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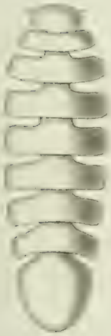

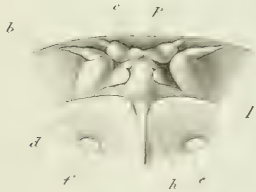

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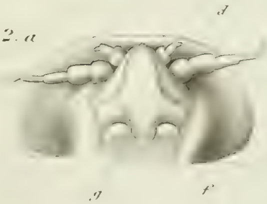

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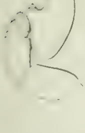

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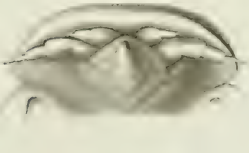

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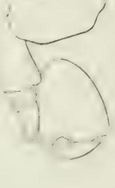

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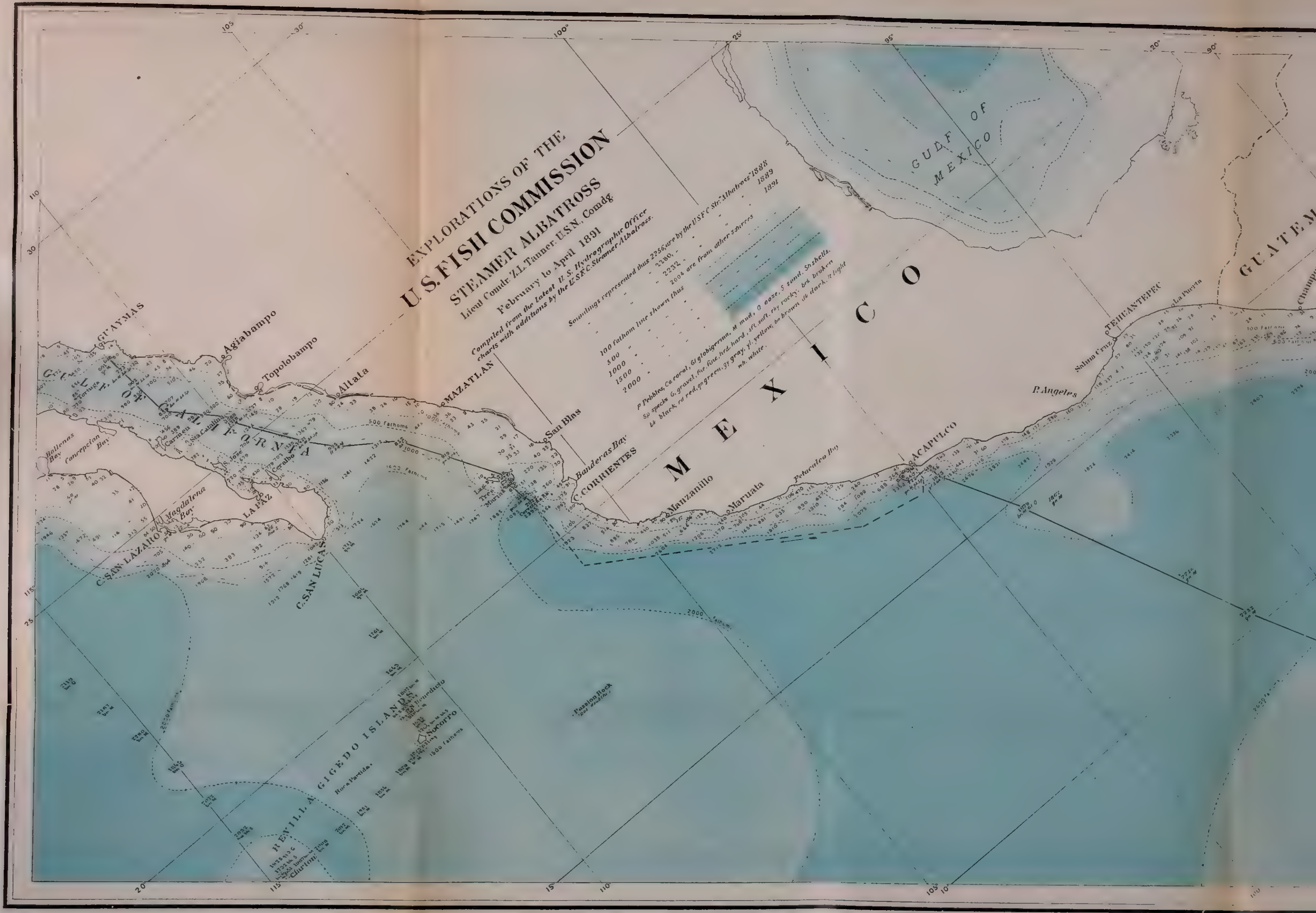
EXPLORATIONS OF THE
U.S. FISH COMMISSION
STEAMER ALBATROSS
Lieut Comdr. Z.L. Tanner. U.S.N., Comdg.
February to April 1891
Compiled from the latest U.S. Hydrographic Office charts with additions by the U.S.F.C. Steamer Albatross.
Soundings represented thus 2256 are by the U.S.F.C. Str. Albatross 1888
2280 1889
2232 1891
2004 are from other sources
100 fathom line shown thus
500
1000
1500
2000
P Pebbles, Co coral, Gl globigerina, M mud, O ooze, S sand, Sh shells, Sp specks, G gravel, fne fine, hrd hard, sft soft, rky rocky, brk broken, bk black, rd red, gn green, gy gray, yl yellow, bn brown, dk dark, lt light, wh white.
MEXICO
GULF OF MEXICO
GULF OF CALIFORNIA
GUATEMALA
GUAYMAS
Agiabampo
Topolobampo
Altata
MAZATLAN
San Blas
Banderas Bay
C. CORRIENTES
Manzanillo
Maruata
Petacalco Bay
ACAPULCO
P. Angeles
Salina Cruz
TEHUANTEPEC
La Puerta
Ballenas Bay
Concepcion Bay
Tortuga
Carmen
Sta. Catalina
S. Jose
Ceralbo
LA PAZ
Magdalena Bay
C. SAN LAZARO
C. SAN LUCAS
Tres Marias
500 Fathoms
1000
1500 Fathoms
2000 Fathoms
Passion Rock
REVILLA GIGEDO ISLANDS
S. Benedicto
Socorro
Roca Partida
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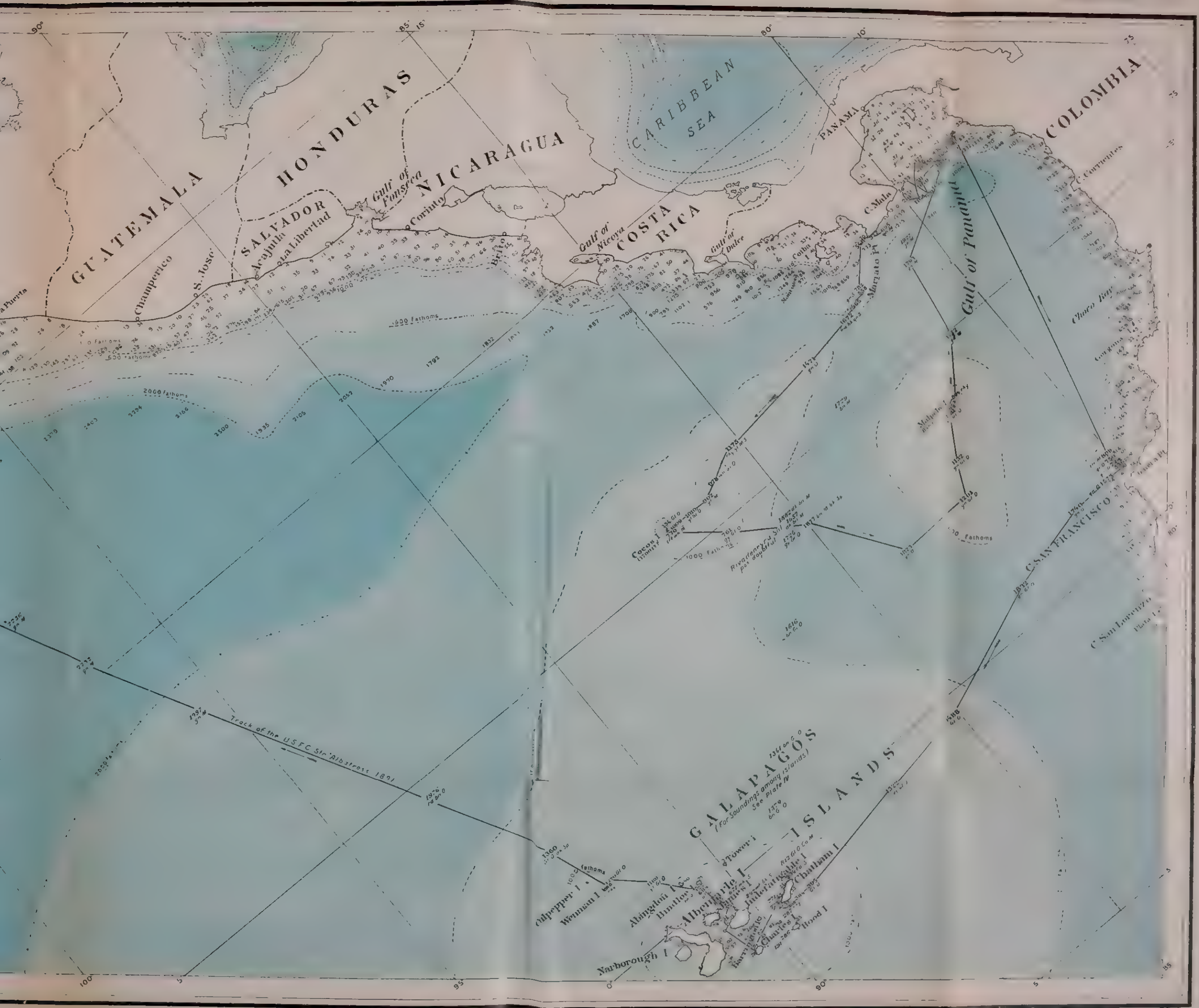
90°
110
115
15
10
105


GUATEMALA
HONDURAS
SALVADOR
NICARAGUA
COSTA RICA
PANAMA
COLOMBIA
CARIBBEAN SEA
Champerico
S. José
Acajutla
La Libertad
Gulf of Fonseca
Corinto
Gulf of Nicoya
Gulf of Dulce
C. Mala
Mariato Pt.
Gulf of Panama
Malpelo I.
C. Corrientes
Choco Bay
C. San Francisco
C. San Lorenzo
Cocos I.
Rivadeneyra Shl. pos. doubtful
500 Fathoms
1000 Fathoms
2000 Fathoms
Track of the U.S.F.C. Str. "Albatross" 1891
GALAPAGOS ISLANDS
(For Soundings among islands) See Plate IV
Culpepper I.
Wenman I.
Abingdon I.
Bindloe I.
Tower I.
Albemarle I.
James I.
Indefatigable I.
Chatham I.
Narborough I.
Charles I.
Hood I.
Barrington I.
90°
85°
80°
75°
100°
95°
15°
10°
5°
0°

No. 6. — *The Thoracic Derivatives of the Postcardinal Veins in Swine.* By G. H. Parker and C. H. Tozier.[1]

Introduction.

Although the postcardinal veins[2] in swine were originally studied by Rathke, and have since been reinvestigated by Hochstetter, our knowledge of them is admittedly fragmentary; for Hochstetter himself regrets that his results in the main do little more than raise doubt as to the accuracy of some of the most important of Rathke's statements, without giving grounds enough for full criticism. It is our purpose in this paper to present what seems to us a consistent account of the changes that these veins undergo, and to offer some critical comments on the questions raised by Hochstetter.

In dealing with this subject we have had recourse to the two general methods of serial sections and injection. The smaller embryos were cut into serial sections, and the courses of the veins then studied by a simple method of graphic reconstruction. The larger ones were injected with a raw starch-mass, or a celloidin-mass. In the former case the veins were afterwards dissected out; in the latter, corrosion preparations were made by dissolving away the tissues of the embryo in an artificial digesting fluid, thus leaving the courses of the vessels indicated by the celloidin. From embryos of intermediate size both reconstructions and injections were made, and the results obtained by the two methods compared.

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, E. L. Mark, Director, No. LXXXVII.

[2] Some little confusion exists as to the terminology of the principal veins in lower vertebrates and the homologues of these veins in mammalian embryos. The principal veins from the head of a fish are usually designated by comparative anatomists as right and left anterior cardinal veins, and their homologues in the mammalian embryo are generally named by embryologists right and left jugular veins. For these veins, whether they be in the adult fish or in the embryonic mammal, we propose to use the names right and left precardinals. In a similar way, the blood-vessels designated by comparative anatomists as right and left posterior cardinal veins, and by embryologists simply as right and left cardinal veins, will be called by us right and left postcardinals. These changes are in harmony with those by which the longer and older names, vena cava posterior and vena cava anterior, have been replaced by postcava and precava, and it is therefore hoped that they will commend themselves alike to embryologists and comparative anatomists.

Observations on Swine.

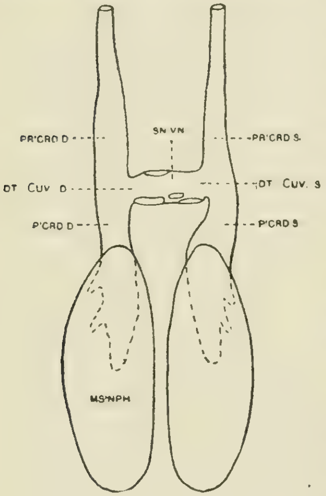

FIGURE 1.

In an embryonic pig, whose greatest length as measured in a straight line from the crown of its head to the root of its tail, was between six and seven millimeters, a reconstruction of the primary veins of the trunk, when viewed ventrally, appeared as in Figure 1. From the anterior end of the embryo, two veins, the right and left precardinals (*pr'crd. d.* and *pr'crd. s.*), pass posteriorly to the region of the heart, where each is met by a corresponding postcardinal (*p'crd. d.* and *p'crd. s.*). The pre- and postcardinals of either side unite to form transverse trunks, the right and left Cuvierian ducts (*dt. Cuv. d.* and *dt. Cuv. s.*). The ducts thus formed unite with each other, giving rise to the venous sinus (*sn. vn.*), through whose posterior wall three large veins enter from the liver, and in whose anterior wall the passage to the heart is seen.

Of these veins the postcardinals (*p'crd. d.*, and *p'crd. s.*) claim our special attention. At this stage they are symmetrical. Each begins posteriorly by a union of several small veins at the base of the hind leg of its own side of the body, and in a region dorsal and lateral to the mesonephros (*ms'nph.*) of the same side. From this region the vein extends anteriorly over the dorsal surface of the mesonephros, penetrating more or less completely the anterior end of that organ, and emerging from it to pass directly, as a well defined blood-vessel, to the Cuvierian

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FIG. 1. Reconstruction on a frontal plane of the principal veins and the mesonephroi of an embryonic pig between six and seven millimeters long. Ventral view. × 12. *dt. Cuv. d.*, right Cuvierian duct; *dt. Cuv. s.*, left Cuvierian duct; *ms'nph.*, mesonephros; *p'crd. d.*, right postcardinal; *p'crd. s.*, left postcardinal; *pr'crd. d.*, right precardinal; *pr'crd. s.*, left precardinal; *sn. vn.*, venous sinus.

duct of the corresponding side. The partial penetration of the mesonephros by the postcardinal might with equal propriety be described as a partial intrusion of the mesonephros into the cavity of the vein, for the loosely twisted nephridial tubules hang with such freedom into the venous blood-spaces that they may with justice be said to occupy more or less of the cavity of the vein itself. This peculiar suspension of the tubules in the venous blood-spaces, a condition which persists in the later stages, has been recently noticed by Minot ('98, p. 229).

In an embryo whose greatest length (measured as before described) was between twelve and thirteen millimeters the veins just considered present the condition shown in Figure 2. Excepting for differences of size, and slight changes in outline, the precardinals are essentially the same as in the preceding stage. In the region of the venous sinus the hepatic opening, which is now single, and the anterior opening, which leads into the heart, have shifted somewhat toward the right side of the body, and the root of a coronary vein (*vn. cor.*) has been formed.

The postcardinals are very much altered. With the growth of the mesonephroi, they have become entirely interrupted in the middle part of their course; their posterior portions, however, persist near the base of the hind legs, finding an outlet toward the heart through the newly formed postcava, and their anterior portions now begin at the anterior ends of the mesonephroi, and each extends to the Cuvierian duct of its own side. The anterior portion of each postcar-

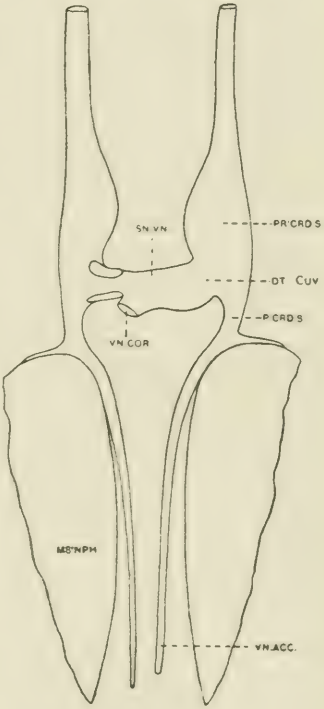

FIGURE 2.

FIG. 2. Reconstruction on a frontal plane of the principal veins and parts of the mesonephroi of an embryonic pig between twelve and thirteen millimeters long. Ventral view. × 12. *dt. Cuv.*, Cuvierian duct; *ms'nph.*, mesonephros; *p'crd. s.*, left postcardinal; *pr'crd. s.*, left precardinal; *sn. vn.*, venous sinus; *vn. acc.*, accessory vein; *vn. cor.*, coronary vein.

dinal receives blood not only from the anterior end of the mesonephros but from the region between the two mesonephroi. This is accomplished, however, not by the postcardinal proper, but by a new outgrowth that takes its origin from the postcardinal near the anterior end of the mesonephros. The walls of these new vessels, which may be called the accessory veins (*vn. acc.*), are extremely delicate; the exact places of union between them and the postcardinals is indicated not only by the general topography, but also by the rather abrupt change in the thickness of the walls where the accessory vessel meets the postcardinal. Moreover, the cavities of the accessory vessels are not freely open throughout their whole extent, as those of the postcardinals are, but are here and there partly interrupted by flattened trabeculæ. In fact, posteriorly these trabeculæ become so numerous that the cavities of the vessels are finally merged in the interspaces thus formed. The accessory vessels at this stage may be traced posteriorly to a point about midway the length of the mesonephros.

In slightly smaller embryos the accessory veins are much shorter, but even in these they always open freely into the postcardinals, and we therefore believe them to be outgrowths of the postcardinal vessels. The place of union between the accessory vessels and the postcardinals in the specimens studied was at the level of the tenth rib, and the accessory vessels could usually be traced posteriorly some distance beyond the last or fourteenth rib.

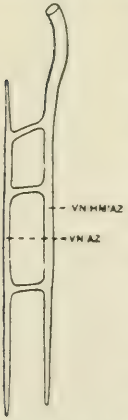

FIGURE 3.

In an embryo whose greatest length was about forty-eight millimeters, the postcardinal and the accessory constituents of each vein could no longer be distinguished, for they had fallen so well into line with each other that they were represented by a perfectly continuous vein (Figure 3). That on the left side, which may now be called the hemiazygos vein (*vn. hm'az.*), retained its earlier connections and extended from the left Cuvierian duct along the left side of the vertebral column to a point some distance posterior to the last rib. That on the right side, the azygos vein (*vn. az.*), had lost its anterior connection with the right Cuvierian duct, but otherwise extended over a tract corresponding in the main to that of the hemiazygos. The blood collected

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FIG. 3. Reconstruction of the azygos and hemiazygos veins from an embryonic pig about forty-eight millimeters long. Ventral view. × 12. *vn. az.*, azygos vein; *vn. hm'az.*, hemiazygos vein.

by the azygos vein was transferred by transverse connecting vessels to the hemiazygos, by which it was carried to the heart. In the specimen from which the reconstruction shown in Figure 3 was made, three such transverse connections were found. In a specimen fifty-five millimeters long, studied by injection, five such vessels occurred, and these were so placed that their ends were opposite the mouths of the newly forming intercostal veins.

The most striking peculiarity of the stage illustrated by Figure 3 is its lack of symmetry. In the earlier conditions described these veins have been bilaterally symmetrical; but with the loss of connection between the azygos and the right Cuvierian duct this symmetry disappears, and a connection with the heart is retained only through the left side. In this respect the pig and probably all ruminants differ from other mammals, in which as a rule the azygos, not the hemiazygos, retains its original connection with the heart.

The further changes that the azygos and hemiazygos undergo may be seen in pigs ranging in length from seven to twenty centimeters. The chief features of these changes consist in the further reduction of the azygos, together with the retention of the transverse connecting vessels, by which the right intercostals are brought to connect directly with the hemiazygos. Depending upon the way in which the azygos is reduced, three types can be distinguished. These are illustrated in Figure 4.

In the first type (Fig. 4, A) the hemiazygos reaches from the heart posteriorly to the eleventh intercostal space, receiving in its course the intercostal veins on the right from the sixth to the eleventh, and on the left from the fifth to the eleventh. Posterior to the eleventh intercostals two longitudinal veins appear, which are of about equal size, and extend posteriorly two segments farther, receiving the twelfth and thirteenth intercostals. Of these the left one (*vn. hm'az.*) obviously represents the posterior continuation of the hemiazygos, the right one (*vn. az.*) the last remnant of the azygos, which in the region of the eleventh intercostal still retains its transverse connection with the hemiazygos.

In the second type (Fig. 4, B) the hemiazygos (*vn. hm'az.*) extends as the predominant vessel from the heart to the fourteenth intercostal space. The azygos is entirely suppressed, except for a small part running from the twelfth to the thirteeth intercostal and possessing at its two ends transverse connections with the hemiazygos.

In the third and last type (Fig. 4, C) the hemiazygos is a well developed trunk from the heart to the ninth intercostal, beyond which the blood is conducted in the main through what is obviously the persistent azygos (*vn. az.*), though remnants of the hemiazygos occur between the ninth and tenth right intercostals, as well as between the eleventh and twelfth.

Thus in the three types considered the anterior part of the system is always formed exclusively from the hemiazygos. The posterior part may be derived from the equally persistent azygos and hemiazygos (type one) or from a preponderant hemiazygos (type two) or finally from a preponderant azygos (type three).

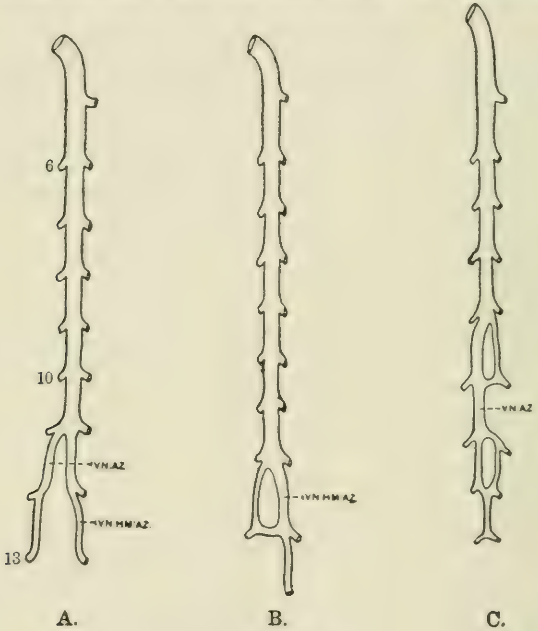

FIGURE 4.

FIG. 4. The hemiazygos and connected veins, showing three structural types. Raw starch injections. Ventral views. *vn. az.*, azygos vein; *vn. hm'az.*, hemiazygos vein; 6, 10, 13, bases of the sixth, tenth, and thirteenth intercostal veins respectively.

A. Type one, with equally persistent azygos and hemiazygos. From an embryonic pig about seven centimeters long. × 3.

B. Type two, with preponderant hemiazygos. From an embryonic pig about eleven centimeters long. × 2.

C. Type three, with preponderant azygos. From an embryonic pig about twenty centimeters long. Natural size.

It will be recalled from the earlier part of this description that the two components (postcardinal and accessory vein) which make up the azygos and the hemiazygos were united at about the level of the tenth rib. The hemiazygos from the region of the heart to the tenth rib is therefore to be regarded as the persistent anterior portion of the left postcardinal. As the corresponding part of the azygos has aborted, the right postcardinal of this region is entirely absent. Consequently the variable portion of this system — most of which lies posterior to the tenth, or at least to the ninth rib — represents the parts derived from the accessory veins.

Although the main stem of the hemiazygos from the heart to the region of the tenth rib has been stated to be derived exclusively from the left postcardinal, it is possible that occasionally a portion of its posterior extent may come from a fusion of both right and left postcardinals; for in one instance we found between the levels of the ninth and tenth intercostals (compare Fig. 4, C) an "island" formation which was so narrow that the right and left components may be said to have almost completely united. While the rareness of such cases makes it improbable that a process of fusion is at all usual, the possibility of its occurrence cannot be ignored, and, where fusion does occur, the incorporation of a part of the right postcardinal into what becomes the main stem of the hemiazygos is at least a possibility. Aside from this, however, the right postcardinal certainly plays no part in the ultimate formation of the system of veins under consideration.

Historico-critical Remarks.

The postcardinals of swine were first described by Rathke ('30, p. 64), whose account, though mainly taken from the sheep, applies, according to this author, almost equally well to the pig. The same account was subsequently somewhat amplified and published by Rathke ('32, p. 82) in a second paper. In both these papers the postcardinals are called posterior venæ cavæ (hintere Hohlvenen), for Rathke believed at this time that the right postcardinal persisted throughout its whole extent as the adult postcava. He further believed that the thoracic portion of the left postcardinal became the hemiazygos. This interpretation agreed well with the fact that, as Rathke ('30, p. 67) pointed out, adult sheep and pigs have no azygos veins, structures that might be supposed to represent the right postcardinals. Stark, as we gather from the historical account given by Hochstetter ('93, p. 611), subsequently showed that in embryonic sheep, in addition to a postcava, an azygos vein also occurred. Rathke seems to have become cognizant of this fact, for in his third paper on this subject he abandoned his earlier views on the fate of the postcardinals, and, without stating reasons for the change, adopted views more nearly in accordance with the new observations made by Stark.

According to Rathke's ('38, pp. 3, 4, and pp. 10, 11) later view, the anterior thoracic portion of the left postcardinal is involved in the formation of the hemiazygos, and the right postcardinal in a similar way enters into the formation, not of the postcava, but of the embryonic azygos. This view agrees in the main with the results obtained by recent investigators (Hochstetter, '93, and Zumstein, '96, '97) on other mammals, and is abundantly confirmed by our own observations on swine.

The facts thus far stated are only a partial exposition of Rathke's later opinion. Only the anterior portions of the azygos and hemiazygos are formed, according to Rathke's later view, from the postcardinals, the posterior parts being developed from a system of longitudinal anastomosing trunks between the successive intercostal veins. These anastomosing trunks receive the blood from the intercostals, passing it forward towards the heart, and thus form a longitudinal vessel, which gradually replaces a part of the original postcardinal. The extent to which this replacement occurs may be indicated as follows. The part of the hemiazygos extending from near the heart to the sixth intercostal vein represents a persistent part of the postcardinal, and the remaining part from the sixth intercostal posteriorly to the last one is a new formation from the longitudinal anastomosing vessel; the part of the embryonic azygos from its connection with the heart posteriorly to the eighth or tenth intercostal represents the right postcardinal, the remaining posterior portion having been derived from the longitudinal anastomosing vessel of that side. After the right intercostals establish transverse connections with the hemiazygos, the azygos disappears, thus leaving the hemiazygos as a return trunk for the blood from the right as well as from the left intercostals.

That the posterior portions of the azygos and of the hemiazygos in many mammals are new formations added to the remnants of the postcardinals is now, we believe, generally admitted, and, as we ourselves have seen, is certainly true for swine; but that these new formations, the accessory veins, develop from anastomosing branches between the intercostal veins, as stated by Rathke, is not, we believe, in accordance with fact. Of the several embryos examined by us at the stage in which the accessory veins were developing, no trace of intercostals or intercostal anastomoses could be discovered, but the accessory veins grew at their posterior ends by a process that seemed like the formation of an opening through the tissues independent of any pre-existing blood-cavities. We therefore believe that Rathke was in error in ascribing to the non-cardinal parts of the azygos and hemiazygos veins in swine an origin from intercostal anastomoses.

In justice to Rathke, however, it should be mentioned that longitudinal anastomosing vessels between the intercostals do occur in embryonic pigs. We have never identified these in early stages, but their presence can be easily demonstrated in older embryos by means of celloidin injections that have been converted into corrosion preparations. In a pig about six centimeters long, the veins between the ninth and eleventh intercostals, when thus prepared and viewed from the dorsal side, are represented in Figure 5. From the longitudinal hemiazygos (*vn. hm'az.*) pass off on the left the three intercostals 9, 10, and 11; on the right, intercostal 11 and intercostal 9, to which intercostal 10 is attached by a longitudinal trunk (*vn. az.*), which probably represents a part of the once complete azygos.

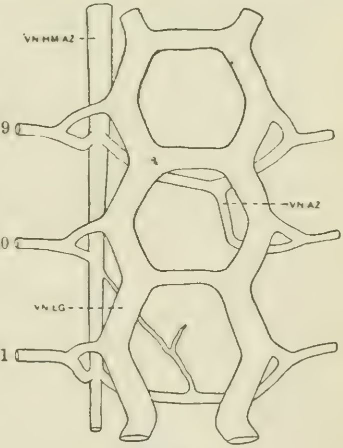

FIGURE 5.

Each of the six intercostal veins mentioned gives off a short dorsal vessel, which opens into a zigzag longitudinal trunk (*vn. lg.*) of the corresponding side of the body. Thus the intercostals of a given side are put into communication with one another by a longitudinal anastomosing trunk. The right and left anastomosing trunks are moreover connected transversely, at regular and frequent intervals, in regions where their inwardly directed angles approach each other, thus producing a series of more or less hexagonal "islands" bounded by blood-

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FIG. 5. The hemiazygos and connected veins from the region of the ninth to the eleventh intercostals in a pig about six centimeters long. Celloidin injection freed by artificial digestion. Dorsal view. × 10. *vn. az.*, azygos vein; *vn. hm'az.*, hemiazygos vein; *vn. lg.*, longitudinal anastomosing vein; 9, 10, 11, respectively ninth, tenth, and eleventh intercostal veins of the left side.

spaces. This system of longitudinal anastomosing vessels may be traced through at least the whole length of the thorax, and lies only a little dorsal to the region occupied by the hemiazygos, being thus in the neighborhood of the forming vertebral column. It seems to us highly probable that these anastomosing vessels were the ones seen by Rathke, and supposed by him to enter partially into the formation of the azygos and hemiazygos veins, a conclusion which, though in our opinion erroneous, is nevertheless not surprising when one considers the methods of investigation employed in his time. What the origin of these vessels may have been and what their subsequent fate may be have not been determined by us, but that they contribute nothing to the formation of the azygos or of the hemiazygos we feel perfectly assured.

The development of the azygos and hemiazygos veins in swine conforms, then, in general to that found by Hochstetter ('93) and by Zumstein ('96, '97) in other mammals.

In one respect, however, there is in this connection still ground for difference of opinion among recent students; this has to do with the proportions in which the postcardinal and accessory components enter into the formation of the azygos and hemiazygos. According to Zumstein ('96, p. 601), in the human being the azygos and the hemiazygos, if there be one, are formed from the postcardinals exclusively, whereas in the Guinea pig (Zumstein, '97, p. 188) both vessels are almost entirely formed from the accessory veins. In the rabbit, and probably also in the cat, according to Hochstetter ('93, pp. 589 and 595), the plane of separation between the two components lies in the eighth thoracic segment, and this agrees very nearly with our observations on swine, where it lies near the tenth pair of ribs. These differences, which are clearly not fundamental, are more likely due to peculiarities in the development of the respective species than to errors of observation, though such topographical determinations are by no means simple.

Conclusions.

1. Small embryonic pigs possess well developed right and left postcardinals (posterior cardinal veins), which extend from the bases of the corresponding posterior extremities anteriorly over the dorsal surfaces of the mesonephroi to the Cuvierian ducts.

2. The thoracic portion of each postcardinal persists from the heart to the region of the tenth pair of ribs, beyond which a new vessel, the accessory vein, is developed to a point some distance posterior to the last pair of ribs.

3. The united postcardinal and accessory veins of the right side give rise to the azygos vein; those of the left side, to the hemiazygos.

4. The azygos and hemiazygos veins receive the intercostal veins of their respective sides and become mutually connected by several transverse veins.

5. The cardinal portion of the azygos vein usually degenerates completely, and the right intercostal veins formerly connected with it then find an outlet through the corresponding part of the hemiazygos, which persists in the adult pig.

6. The accessory parts of the azygos and hemiazygos veins may remain connected with the cardinal part of the hemiazygos, and by their variations give rise to three structural types: first, one in which both accessory parts are equally developed; secondly, one in which the hemiazygos accessory predominates; and thirdly, one in which the azygos accessory predominates.

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No. 7. — *The Segmentation of the Nervous System in Squalus acanthias. A Contribution to the Morphology of the Vertebrate Head.*[1] By H. V. Neal.

CONTENTS.

Page
Introduction 148
  Criteria of Segmentation 148
  Summary of Results of former Investigations on the Segmentation of the Encephalon 150
  I. Locy's "Neural Segments" or "Metameres" 154
    a. Material 154
    b. Method of Study 155
    c. Description of Locy's "Neural Segments" 156
    d. Continuity of the "Segments" 159
    e. Interpretation of the Evidence 161
    f. Limit of "Cephalic Plate" . 162
  II. The "Hindbrain Neuromeres" in S. acanthias 166
    a. Definition of the Term "Neuromere" 166
    b. Development of Hindbrain Neuromeres 167
    c. Summary 172
  III. The Neuromeres in the Trunk Region 173
    a. Development of Myelomeres 173
    b. Summary 176
  IV. The Neuromeres anterior to the Hindbrain 177
    a. Essential Criteria of Neuromeres 177
    b. Development of the Forebrain and Midbrain . . . 179
    c. Summary 185
  V. The Relation of Neuromeres to Somites 186
    a. Relation of Myelomeres to Somites 186
    b. Relation of Encephalomeres to Somites 187
    c. Somatic Value of the Pre-otic Mesoderm Segments . . 187
    d. Summary 206
  VI. The Relation of Neuromeres to Nerves 207
    a. Historical Review . . . 208
    b. Nerve Relations in the Trunk of S. acanthias . . 210
    c. Nerve Relations in the Cephalic Region 211
    d. Development of the
      1. Oculomotorius . . . 220
      2. Abducens 230
      3. Trochlearis 235
  VII. Segmental Value of Hindbrain Neuromeres 240
    a. Non-phylogenetic Interpretation 240
    b. Phylogenetic Interpretation 243
    c. Interpretation of Hindbrain Neuromeres in S. acanthias 245
  VIII. Primitive Relations of Cephalic Segments I.–VII. . . . 254
    a. Encephalomere VII. . . . 254
    b. Encephalomere VI. . . . 255
    c. Encephalomere V. . . . 255
    d. Encephalomere IV. . . . 256
    e. Encephalomere III. . . . 258
    f. Encephalomere II. . . . 258
    g. Encephalomere I. 259
    h. Comparison with the Segmentation of Amphioxus . 260
    i. General Conclusions . . . 268
  IX. Summary 275
Bibliography 279
Description of Plates 293

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[1] Contributions from the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College, under the direction of E. L. Mark, No. LXXXIX.

Introduction.

CRITERIA OF SEGMENTATION.

MORPHOLOGISTS have long sought to compare in Vertebrates a head segment with a trunk segment. They have assumed that in the ancestors of Vertebrates head and trunk were differentiated from each other, and that similar segments once extended throughout the entire length of the body. Direct evidence in favor of this assumption is now furnished, it is held, by Amphioxus. Because of the many difficulties involved, the problem has become a favorite one, and since the early attempts made by the poet Goethe and anatomists of the "Transcendental" school, many men have contributed evidence and theory in the hope of its solution. Since Goethe and Oken maintained the bony cranium to be composed of fused vertebræ comparable with those in the vertebral column, the problem has passed through several phases. First, Huxley ('58), upon broad comparative anatomical evidence, proved that nothing like a vertebra is to be found in the cranium of either high or low Vertebrates, and he concluded as a result of his researches that morphologists, in attempting to find a primitive metamerism in a structure which is so late in its phylogenetic appearance as the bony cranium, were approaching the problem in the wrong direction. In thus disproving the "vertebral theory" of the Vertebrate cranium, however, "war die Frage doch noch nicht aus der Welt geschafft," as Gegenbaur wrote in his famous "Kritik." By Gegenbaur ('72) the question was transformed into a problem of the phylogenesis of the *entire* head. By using as criteria the visceral arches and the nerves which innervate them, he attempted to determine the number of primitive segments in the head of those low Vertebrates, the Selachii, which in his opinion most resembled the hypothetical Vertebrate ancestors.

With the gradual acceptance of the "fundamental law of biogenesis," that the development of an individual is an epitome of the development of the race, the evidence offered in the solution of the problem of the morphology of the Vertebrate head has become more and more embryological.

After Balfour's ('78) discovery that the primary body cavity of Selachian embryos extends unbroken into the head region, and the further discovery of Marshall ('81) that in these embryos the body cavity of the head undergoes an independent segmentation into mesodermal cavities, Selachian embryos became the chief objects of research. It was finally left to van Wijhe ('82) to demonstrate in Selachian embryos an uninterrupted continuity, and a direct morphological comparability, of head and trunk "Mesodermsegmente," and thus, in the opinion of many morphologists, the existence of an "acraniote" stage in the development of craniote embryos. Since the "mesodermal segments" or somites were regarded as the best evidence of the primitive segmentation, it was at first believed that the problem of the morphology of the Vertebrate head, as regards both number and nature of segments, had at last been solved by van Wijhe. His conclusion was that nine segments, four of which were pre-otic and five post-otic, enter into the formation of the Vertebrate head, or at least the Selachian head.

Yet one who studies the literature of the decade and a half that has elapsed since van Wijhe wrote his famous paper must conclude, from the great divergence of opinion which still prevails among the most competent investigators as regards both nature and number of head segments, that the problem is "noch nicht aus der Welt geschafft." According to Froriep, Kastschenko, and Rabl, the segments of the pre-otic and post-otic regions are of a fundamentally different kind. Furthermore, while Rabl ('92) finds not over three segments in the entire pre-otic region, Dohrn ('90) finds in the same region twelve to fifteen segments, serially homologous with trunk segments. These, indeed, represent extremes of opinion, for the majority of morphologists agree with Gegenbaur and van Wijhe that pre-otic segments are few but comparable with trunk segments. The chief causes of the present disagreement of morphologists are two. In the eager search for evidence of *segments* investigators have often failed (1) to control their results, based upon the study of a single organ system, by a comparison of the *actual* conditions which obtain in other organ systems in the same organism; and (2) to control conclusions based upon a single organism by appeal to the facts and conclusions of comparative anatomy and embryology. As the result of the healthful scepticism of such accurate observers as Froriep, Kastschenko, and Rabl, the necessity for such control now seems too obvious to need repetition here.

While morphologists (excepting Gegenbaur) in attempting to elucidate the problem of cephalic segmentation have based their conclusions chiefly on the study of the mesodermal segments, — since these have seemed to afford the best criteria of segmentation, — yet other embryonic structures have also been studied, viz. the segments of the central nervous system, or "neuromeres," the nerves, the epibranchial organs, the blood-vessels, and the visceral arches.

It is well known that in embryos of all classes of Vertebrates the central nervous system shows a segmentation which consists in a series of constrictions and dilatations extending throughout the length of the neural tube, giving to it a beaded appearance. In the trunk the nerves have a definite relation to the segments of the spinal cord, the "myelomeres," as I shall call them, adopting the term introduced by McClure ('89), and it is believed that the cranial nerves also have definite relations to the segments of the brain, the "encephalomeres," although their relations are less clear. Even if we believe with Ahlborn ('84^a) and Froriep ('94) that the nervous system is segmented in adaptation to associated segmental structures, it is not *a priori* improbable that the number of primitive segments in the Vertebrate may be shown by the number of neural segments, for in some Invertebrate embryos segmental cephalic ganglia appear even when most other traces of mesodermal segments and related sense organs have (it is believed) disappeared.

In view of the present discrepancy between the results based upon the study of neuromerism and those based upon the study of mesomerism, it devolves upon one who attempts to elucidate the question of cephalic segmentation in Vertebrates by using the segments of the central nervous system as criteria, to show the comparability of encephalomeres with myelomeres, not only structurally, but also in relation to nervous outgrowths, and to those divisions of the mesoderm on which the segmentation of the motor nerves ultimately depends. The interdependence of motor nerve and muscle has seemed so evident that morphologists have not hesitated to make the number of cranial nerves conform with the number of somites previously determined by them. Yet the majority of investigators of the segments of the encephalon have failed to take into consideration the relation of these to the segments of the mesoderm, and consequently we find in the literature upon neuromerism a diversity of opinion such as we have learned to expect in results based upon insufficient knowledge.

Summary of Results of former Investigations on the Segmentation of the Encephalon.

The results of former investigators concerning the number of encephalomeres and their nerve relations may be summarized in the form of two tables. Table I. shows the number of segments as determined by previous investigators, as well as their relation to the primary vesicles of the brain. The total number of segments has been given in the cases where it has been stated by the observer. The observations of

Table I. — ENCEPHALIC SEGMENTS.

				F.B.	M.B.	H.B.	Total.
Mammals.	'42	Bischoff	Dog			6	
	'69	Dursy	Ox		3?	6	
	'77	Mihalkovics	Rabbit			5–6	
	'86	Kupffer	Sheep, Mouse, Man			5	
	'89	Prenant	Swine			5	
	'91	Zimmermann	Rabbit	2	3	8	13
	'92, '92^{a}	Froriep	Mole	2	3	7	12
	'95	Broman	Man			7	
Birds.	'55	Remak	Chick			5–6	
	'77	Mihalkovics	"			5–6	
	'85	Rabl	"			6–7	
	'87	Béraneck	"	2	1	6	9
	'89	Platt	"	1	1	6	8
	'90	McClure	"	2	2	6	10
	'91	Zimmermann	"	2	3	8	13
Reptiles.	'84	Béraneck	Lizard			5	
	'87	Orr	"	2	1	6	9
	'85, '89	Hoffmann	"			7	
	'85, '89	Hoffmann	Tropidonotus			7	
	'90	McClure	Lizard	2	2	6	10
	'91	Clarke	Alligator			5	
	'92	Herrick	Snake			5–7	
Amphibians.	'75	Goette	Bombinator			?	
	'86, '93	Kupffer	Salamandra	5	3	?	
	'90	McClure	Amblystoma	2	2	5	9
	'91	Waters	"	3	2	5	10
	'92, '92^{a}	Froriep	Salamandra				4
	'92, '92^{a}	Froriep	Triton				5
	'92	Wiedersheim	Salamandrina	?	?	?	?
Fishes.	'75	Dohrn	Teleostei			8–9	
	'84, '85	Kupffer	"		3	5	
	'87	Scott	Petromyzon		3	5	
	'89	Platt	Salmon			5	
	'91	Waters	Cod	3	2	6	11
	'91	Zimmermann	Acanthias	2	3	8	13
	'93	Kupffer	Acipenser	5	3	5	13
	'94	Kupffer	Ammocœtes		3		
	'94	Locy	Squalus	3	2	6	11
	'95	Locy	"	3	2	6 (8)	14–15

investigators upon neuromerism have been seldom, if ever, so far extended as to determine the number of segments finally included in the head. The reason for this has been that the hindbrain neuromeres disappear before their relations to the posterior limit of the cranium can be determined. Table II. gives the nerve relations in different Vertebrates,

TABLE II. — ENCEPHALIC SEGMENTS AND NERVE RELATIONS.

			F.B.			M.B.		H.B.								
	No. of Segmental Divisions.		1	2	3	1	2	1	2	3	4	5	6	7	8	9
'84	Béraneck	Lacerta							V		{ VII VIII }	Ear	IX ?			
'87	Béraneck	Chick	I	II			III	IV	V	V	"	VI	IX			
'87	Orr	Lizard	I	II			III	IV	V	VI	"	Ear	IX	X		
'89	Hoffmann	Lizard					IV		V		"	"	IX	X–XI		
'89	McClure	Chick	I			III	IV		V		"	"	IX	X		
'89	McClure	Lizard	I			III	IV		V		"	"	IX	X		
'89	McClure	Amblystoma	I			III	IV		V		"	"	IX	X		
'89	Platt	Salmon							V		"	"	IX			
'89	Platt	Chick							V		"	"	IX			
'91	Waters	Cod	I	II		III	IV		V	VI	"	"	IX			
'91	Waters	Amblystoma	I	II		III	IV		V	?	"	"	IX			
'91	Zimmermann	Rabbit	I			III		IV	V		"	VI	IX	X	XI	XII
'91	Zimmermann	Chick	I			III		IV	V		"	VI	IX	X	XI	XII
'91	Zimmermann	Acanthias	I			III		IV	V		"	VI	IX	X	XI	XII
'92	Herrick	Snake							V	VI	"		IX	X		
'92^{a}	Froriep	Mole							V	V	"	Ear	IX	X		
'95	Locy	Squalus	I	II	III	IV		V	V		VII	VIII	IX	X	X	X
'95	Broman	Man				IV				V	VI	{ VII VIII }	IX	X	XI	XII

so far as they have been studied. In both tables it has been impossible to exclude much that is theoretical, and in view of this fact general conclusions are obviously dangerous. One important result, which should be borne in mind during the discussion of the evidence presented in this paper, is established, viz. the constancy, in all classes of Vertebrates, of five "hindbrain neuromeres" ("Falten" or "vrais replis"), and of their nerve relations. When *six* have been counted, usually the Anlage of the cerebellum has been included with them, and when *seven* (see Hoffmann, '90), another fold behind the true fifth neuromere has been counted. There is consensus of opinion that from the third "hindbrain neuromere" (designated in Table II. as 5, and as V in my figures) the acustico-facialis nerve takes its origin. In counting hindbrain neuromeres, then, this may safely be used as a check. In regard to the presence of true neuromeres, comparable with those of the hindbrain, in the region of the encephalon anterior to the hindbrain, much is theoretical, and, as I believe, uncritical. Morphologists have naturally been more or less prejudiced in favor of the view that a serially homologous segmentation extends throughout head and trunk. This preconception has led to the search for resemblances at the risk of disregarding differences which obviously exist, and as a result structures in the encephalon which are morphologically incomparable with the myelomeres have been homologized with them. Moreover, this has been done in utter disregard of their relations to the segments of the mesoderm.

The study of neural segments and their relations to nerves and somites in embryos of Squalus acanthias has given me some facts bearing on the problem of cephalic segmentation, which are, so far as I know, new. The conclusion which I have reached is as follows. *In S. acanthias there exists in early stages a continuous primitive segmentation of the nervous system serially homologous throughout head and trunk, — the "neuromeric" segmentation.* In later stages there appears in the encephalon a secondary (in time) segmentation resulting in the so called vesicles, which are not serially homologous with the segments of the myelon, but give rise to an anterior cephalic tract, which is a region *sui generis.*

In the following discussion I propose (1) to trace the development of neuromeres; (2) to compare the structure of the segments of the encephalon with those of the myelon; and (3) to note the relation of the neuromeres to the sensor and motor nerves, to the mesodermal somites, and to the visceral arches. I shall begin with the description of the first appearance of neural segmentation in the embryo.

I. Locy's "Neural Segments" or "Metameres."

a. MATERIAL.

Much of my material was collected with a view to the study of the "neural segments" or "metameres" described by Locy ('94 and '95). In a preliminary paper, which appeared with numerous illustrations in the "Anatomischer Anzeiger," 1894, Locy affirmed the discovery of "neural segments" in embryos of Squalus acanthias[1] at stages preceding the formation of the medullary folds and "before the mesoblast has, to any extent, become divided into somites." He therefore believed that these "epiblastic segments must be independent of any formative influence of the segments of the mesoblast." This discovery is interesting, and, if confirmed, one of most fundamental importance. I have therefore collected a large number of Squalus embryos in early stages of development, in order to confirm, if possible, Locy's results.

S. acanthias is abundant along the coast of Massachusetts in early summer, and the embryos are very easily obtained. My collecting was done at Rockport, Massachusetts, during the months of July and August, 1894, 1895, and 1896, and the number of specimens obtained exceeds twenty-five hundred. Locy has well insisted on the necessity of abundant material in closely connected stages of development.

The killing agents which I have used were (1) Davidoff's corrosive sublimate-acetic; (2) Kleinenberg's picro-sulphuric (undiluted); and (3) a mixture of Kleinenberg's picro-sulphuric (1 vol.), with ½% chromic acid (3 vol.), especially recommended by Locy.

In this material were more than two hundred and fifty embryos corresponding to Balfour's stages C, D, and E. The specimen which shows Locy's "neural segments" best was killed in Kleinenberg's picro-sulphuric mixture (Plate **1**, Figs. 1 and 2). I cannot recommend the mixture composed of picro-sulphuric and chromic acids, since specimens killed in it were not well preserved histologically. Davidoff's corrosive sublimate-acetic seems to me the best for general purposes of all the killing agents I have used, and consequently most of my material has been so killed. For the special study of the development of the nerves and the fibre courses in the wall of the brain, I have used material killed with vom Rath's fluid, followed by pyroligneous acid. This method I regard as most valuable, since with it nerve fibres are differentiated by the precipitation of osmium in the very earliest stages of development, and it has given me results which I have been able to obtain in no other way. For staining sections Kleinenberg's hæmatoxylin has been used chiefly, while Heidenhain's iron hæmatoxylin and Grenacher's alcoholic borax carmine have both given excellent results.

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[1] Squalus acanthias (Linnæus, 1748), synonymous with Acanthias vulgaris (Risso, 1826).

b. Method of Study.

In studying Locy's "neural segments" in Squalus embryos, reflected light was used, and in consequence low powers of the microscope were necessary. I have used constantly a small Zeiss stand in which the upper half of the stage and the superstructure revolve on the lower half of the stage, and his objective A and ocular I. My method of procedure has been, first, to make with the aid of a camera lucida an outline of the embryo cleared in clove oil and viewed as a transparent object. The irregularities of the edge of the neural plate may thus be represented accurately, and may serve as landmarks in the subsequent study of the specimen as an opaque object. After the outline drawing has been made, the specimen is transferred to a watch glass filled with alcohol. Now the important question is illumination. In order to bring out the delicate structures along the edges of the neural plate, oblique illumination should be used, since it brings into strong contrast the shadows and the high lights. The embryos should be rotated, so that light may be obtained successively from all directions and thus the chance of deception by false lights avoided. As the embryo is studied chiefly from the ventral side (for reasons given by Locy), careful manipulation with brush and needle is necessary in order to remove the yolk, which would otherwise obscure the edges of the neural folds. In studying these surface conditions, I have found a very faint hæmatoxylin stain and a black background to be of advantage.

In representing the specimen under observation, I have not had recourse to photography, but have made as faithful a representation as possible with pencil, seeking to preserve the relative values of light and shade. Since it is possible by careful illumination to increase the contrast of light and shade to a considerable amount, it is well to study the same embryo with different kinds of illumination. In this way it is possible to determine more satisfactorily what is permanent and what is not. The study of the segments is by no means easy, and the labor is considerable because it is necessary to study so many individuals. It is evident from a comparison of Locy's photographic representations, given in his final paper ('95), with his drawings, that the latter are, probably for the sake of clearness, semi-diagrammatic in character. While his photographic reproductions show absolutely no segmentation in the early stages, his drawings on the contrary show in these same stages "segments" as clearly marked as those of later stages. Photography is obviously unsatisfactory as a means of reproducing these delicate structures.

Before taking up the consideration of the evidence which I have obtained from my studies, it is well to give a brief review of Locy's results. In his final paper ('95) he qualified his statement that the segmentation is solely epiblastic, since he discovered in sections that it may be found in both mesoderm and ectoderm. He therefore concludes that the segments seen in surface study are the remnants of a primitive metamerism of the Vertebrate body. The more important points in Locy's description may be briefly summarized as follows. The evidence of segmentation appears first in the non-axial part of the embryo, i. e. along the thickened blastodermic rim. The segments later extend along the lateral margin of the neural plate from the anterior unsegmented tip of the embryo backward into the non-axial part. The segments are most clearly seen in "marginal bands along the neural plate," though "in the trunk region the lines of division may be traced inward toward the median furrow. This is probably due to the appearance of the mesodermic somites in that region." The "marginal bands," he thinks, "represent the dorsal nerve cord."[1] "These segments, once established in this very early stage, may be traced onward in an unbroken continuity until they become the neuromeres of other observers, and sustain definite relations to the spinal and cranial nerves." In the conclusion of his preliminary paper Locy writes, "No one is likely to question but what the segmented condition I have described represents a survival" (i. e. of an ancestral segmentation ?). My own observations on embryos of S. acanthias lead me to question in large part the accuracy of Locy's observations, as well as his interpretations.

c. Description of Locy's "Neural Segments."

I shall now give an account of the conditions, as I have found them, in the head region of a shark embryo with 6 to 6½ somites.[2] This

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[1] In his final paper Locy speaks of the "neural folds or ridges" as "divided throughout their length into a series of segments."

[2] I count the somites beginning with van Wijhe's 7th somite (somite 7 of my figures), the myotome of which becomes the first segment of the lateral trunk musculature (van Wijhe).

stage has been selected to begin with, because it gives the strongest evidence that I have seen of a segmented condition in the neural plate. I shall describe first two embryos which represent fairly well the conditions I have found at this stage. These two embryos are represented in Figures 1, 2, and 3, Plate **1**. The neural or "medullary" plate is seen to be a spatula-like expansion of the anterior end of the embryo, raised somewhat above the blastodermic area. Figure 1 (Plate **1**) represents an embryo viewed from the dorsal side; the neural plate, it will be observed, is not perfectly flat, for its edges bend slightly ventrad and a shallow depression extends along its median portion. The chorda, lying in the axis just beneath the neural plate, causes a slight elevation of the floor of the groove in the median line. Anteriorly the chorda passes into the common tissue which later becomes differentiated into entoderm, mesoderm, and chorda. The anterior more expanded portion of the neural plate has been called the "cephalic plate." At the posterior portion of this cephalic plate its lateral wing-like expansions undergo their greatest bending ventrad. The posterior or trunk portion of the neural plate extends back into the tail folds and along the embryonic rim. I do not wish to seem to imply by this statement that the tail folds and the embryonic rim become included in the neural tube, because, although in general I believe in the concrescence theory, I do not find in the *continuity* stated above any evidence of addition to the posterior part of the neural plate by a concrescence of the tail folds and the embryonic rim.

In the dorsal view of the embryo shown in Figure 1, Plate **1**, little or no evidence is afforded in either cephalic or trunk regions in support of Locy's contention that the edges of the neural plate are segmented. We see only that the edges of the plate are slightly and *irregularly* lobed, and not in the true sense segmented. For *the lobes on the opposite margins of the plate do not correspond in number or position, neither do they show any definite relation to the mesodermal somites, as seen in the cleared specimen.*

Figure 2, Plate **1**, shows the same embryo viewed from the ventral side, and gives the strongest evidence I have seen of Locy's interpretation of the condition of the neural plate. The "segments" appear much more marked in embryos of this stage when viewed from the ventral side, for reasons already stated by Locy, who has well insisted upon the importance of ventral views. There are several reasons, however, for regarding the structures which appear along the edges of the neural plate as not true segments. These so called segments, even in the cephalic region, are not equally distinct, it being very difficult, if not impossible, to determine the boundaries of some of them. They also differ considerably in length and apparently without any regularity, a condition not easily reconciled with the interpretation of them as true segments. It would certainly be impossible even in this specimen to point out with certainty corresponding segments on opposite sides of the cephalic plate. In the trunk region of the same specimen no correspondence between somites and "neural segments" is seen. However, a faint lobing of the inner margin of the tail fold is seen on the right side of the embryo. Locy's ('95, p. 519, Fig. 29) description of a stage as close to this as any figured by him is as follows: "They [the segments] appear like a row of beads running along the ventrally recurved margin, and extend with great distinctness the entire length of the embryo. Those in the trunk region are continuous with those of the head, and pass into the latter without any transition forms. There is, however, some individual variation in size of the neuromeres, and they are not absolutely symmetrical on the right and left sides, but the significant thing is, [that] there is uniformly the same number on each side in a given region, such as the hindbrain, or the brain region as a whole. . . . There seems now to be a natural landmark separating the 'cephalic plate' from the rest of the embryo; this is an abrupt downward bending in the medullary folds, which, as I have determined, lies just in front of the future origin of the vagus nerve. There are eleven *metameres*[1] in the lateral margins of the cephalic plate, including the ones embraced in this fold." The accuracy of this conclusion I shall discuss in treating of the question of the limit of the cephalic plate (p. 162). I wish here only to call attention to the fact that none of the reproductions of Locy's photographs, with two possible exceptions (his Figs. 2 and 23), show a segmentation of the neural folds in either the trunk or the embryonic rim.

If now we turn to Figure 3 (Plate **1**), we find an embryo of about the same stage as that shown in Figures 1 and 2; at least, it has the same number of somites (6 to 6½). The conditions are these. The "segments" at the margin of the neural plate differ markedly in distinctness, and are irregular in size. In the region of the cephalic plate — the posterior boundary of which is marked by the arrow — the number of segments on the right and left sides is not the same. I was not able to assert this with so much confidence in regard to the embryo of Figures 1 and 2, since in that embryo the limits of the cephalic plate were less clearly defined. If the segments of the two sides of the neu-

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[1] Italics mine.

ral plate in Figure 2 do not admit of a satisfactory comparison, neither is it possible, even with a prejudice in favor of finding uniform conditions, to state exactly which segments of Figure 3 correspond to those of Figure 2.

An examination of many embryos (more than fifty) in this stage of development — at which, in agreement with Locy, I have found that the segments are more clearly marked than at any other stage — has served only to establish the opinion that there is no constancy in their number in different individuals, nor agreement in number or position upon the two sides of the plate of a single individual. After an examination of a large number of embryos at this and closely related stages, I have been compelled to abandon my first opinion, which was based chiefly on the study of the embryos of Figures 1 and 2, and was favorable to Locy's contention. In no case that I have seen do the segments appear symmetrical, and in no case have I been able to determine a definite relation with the somites.

d. Continuity of the "Segments."

My observations have of course not been confined to this most favorable stage. While the evidence given above, based on the study of embryos at a stage when the segments are most plainly seen, appears to my mind satisfactory proof that true segments do not exist at this time, the study of embryos in both earlier and later stages shows that even these segments are only transitory structures. This evidence, though in a sense negative, is not without weight in the treatment of the question. It constitutes, it is true, neither proof nor disproof of the genuineness of the segments. It is, however, what we should expect, if we find the segments unlike in number and size on the two sides of the same embryo and in different embryos of the same stage. A want of continuity in successive stages is not, however, what we should expect if we were dealing with true segments. These structures would certainly have much less morphological value than is assigned to them by Locy, were they simply transitory and without definite relation to organs which appear in later stages. Locy believes that he has traced them "up to the time when they form neuromeres," but he by no means makes it clear how structures which appear "like beads" along the edges of the neural plate become transformed into *ventral* structures such as, according to his own account, the "neuromeres" are. "In the trunk region," he says ('95, p. 516), "the lines of division may be traced inwards toward the median furrow. This is probably due to the appearance of the mesodermic somites in that region." In the head region, where somites do not similarly press upon the neural plate, it still remains for Locy to show how structures morphologically dorsal, as his "neural segments" are, become converted into structures morphologically ventral as well as dorsal, as are the "hindbrain neuromeres," for example.

My own evidence of their continuity in time is, as I have said, negative. Figure 4, Plate **2**, represents an early stage with three or four somites. One sees the "marginal bands" of which Locy has spoken, but only the faintest traces of segments are visible. On one side — the right — they are exceedingly irregular. At this stage the lateral edges of the neural plate are not flexed ventrally, and such segments as are to be seen at all show best from the dorsal side. A quite regular segmentation is seen on the left side of the cephalic plate, yet the segments are by no means all of the same size or distinctness, nor do they equal in size the mesodermal segments. In the trunk region the lobes of the edge of the neural plate show no definite relation to the mesodermal somites, the boundary between two somites coinciding in some cases with the depression between lobes, in others with the apices or with other parts of the lobes. I wish to call especial attention to the fact that here, as in the embryos shown on Plate **1**, *the segments are confined to the marginal bands*, and therefore do not extend into the median plate. Here, again, there is a considerable discrepancy between Locy's observations and my own.

I have found it impossible to trace definite segments into the later stages, for in these stages, before the closure of the neural tube, in the majority of specimens little or no evidence of segments along the cephalic plate can be seen.

Two embryos in later stages of development are seen in Figures 5 and 6, Plate **2**. There is practically no evidence of segmentation or lobing of the edge of the medullary folds. The segments which Locy has numbered 1, 2, and 3 are visible in many specimens, in some very distinctly, as shown in his photographs; but behind them there is an irregularly sinuous or entirely smooth edge, as shown in my Figures 5 and 6, and in Locy's photographic reproductions. These three anterior segments, according to Locy, shift their position. Since, however, I do not find them constant in appearance and position, I have not been able to regard them as of morphological importance. It is worthy of note that they appear in the region of the neuropore, and that possibly they may be partly accounted for as the result of the difficulty of fusion of the neural folds at this point (the angulus terminalis). Their late appearance is possibly also to be correlated with the late appearance of the anterior portion of the neural crest.

The evidence which I have given leads me to conclude that the so called neural segments cannot be traced into the "neuromeres" of later stages. Of the accuracy with which Locy has traced them I shall have more to say, when I speak of the limits of the cephalic plate.

e. INTERPRETATION OF THE EVIDENCE.

Locy interprets the "neural segments," as has already been stated, as "survivals of a primitively segmented condition of the body." In search for evidence to support this phylogenetic interpretation, he has studied the early stages of the Torpedo, Amphibia is, and the chick.

Torpedo embryos (p. 531) are found to be "not so favorable for the study of the segments as Acanthias," yet "the number [of folds] in a given region in Torpedo corresponds to that in Acanthias." In the three Amphibian forms which Locy has studied (Amblystoma, Diemyctylus, and Rana) "there are *about* ten pairs of segments in the broadly expanded neural folds of the head." In the chick, "there are eleven segments in front of the first formed protovertebræ." Locy has also found (p. 539) that in the chick "*the walls of the primitive groove are also divided into segments that are similar to those that appear in the neural folds.*"[1]

Owing to the evidence stated above, I am unable to regard the segments in S. acanthias as of phylogenetic value. Are they then artifacts, as suggested by Eycleshymer?[2] I do not think so. Several of the best fixing agents have been used by Locy and myself, and he has in addition observed these structures in living embryos. It is known, however, that different fixing agents cause differences in internal and external conditions, as the result of swelling or contraction. They may have served to intensify the distinctness of Locy's segments, yet it is hardly probable that they are the sole cause of them.

I believe that the segments are the results of unequal growth along the margin of the neural plate. It is obviously not necessary to

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[1] Italics my own.

[2] Eycleshymer's ('95, p. 394) observations on Amblystoma do not agree with those of Locy. Eycleshymer states that "certain markings which might be interpreted as neuromeres are often observed in the neural folds, yet their arrangement is decidedly irregular, and one is led to believe that they indicate nothing more than artifacts caused by the killing agents." I have carefully examined Amblystoma embryos, at a stage when the neural folds are widely open, and my observations agree with those of Eycleshymer.

regard such irregularities of the edge of a rapidly expanding plate of tissue as of morphological importance. It is very significant that the segments show most prominently in the cephalic-plate region just before the edges of the plate begin to rise dorsally, for it is likewise at this stage that I find the first evidence of the disassociation of cells along the edges of the neural crest. Such a disassociation of cells, or even a rapid proliferation of cells, — which certainly does occur in this region, — would lead to such phenomena as those reproduced in Figures 1 and 2, Plate **1**. An examination of cross sections of the cephalic plate (Plate **7**, Figs. 55 and 56) before the edges have fused dorsally to form a closed tube shows that the neural crest is already differentiated from the tissue which will form the walls of the neural tube; it is differentiated as a region of rapid cell proliferation and of less compactly arranged nuclei. If the centres of cell proliferation were fixed, then we should have a segmented neural ridge, as affirmed by Beard ('88).

My interpretation differs from Locy's, since he finds the "neural ridges" segmented regularly, and considers the segments as survivals of an ancestral segmentation; whereas I find the edges of the neural plate irregularly and somewhat transitorily segmented, the irregularity and inconstancy of the segments precluding, in my opinion, a phylogenetic interpretation. Locy's results from surface studies seem to me to be a confirmation of those reached by Beard ('88), who, in studying the development of the peripheral nervous system in Selachii, found from the examination of sections that the neural crest is differentiated before somites appear, and that it is from the beginning segmented. Beard's conclusions have, however, never been confirmed, and have indeed been regarded by Dohrn ('90, p. 55) as quite untenable.

To demonstrate that Locy has not accurately traced the "neural segments" onward in unbroken continuity until they become the "neuromeres of other observers," I propose to discuss the relation of the neuromeres to the posterior limit of the cephalic plate.

f. LIMIT OF "CEPHALIC PLATE."

Locy ('95, p. 543) has stated that in early stages of the embryo, before the neural plate has formed a closed tube, head and trunk may be distinguished. "It is possible," he says, "in very young stages to draw a line indicating where the expanded part of the cephalic plate joins the non-expanded part of the embryo. . . . This is, in Squalus acanthias, just in front of the point where, subsequently, the vagus nerve begins. . . . In this animal, we may identify that part of the head which lies in front of the vagus nerve by counting the first eleven neural segments. It will be merely a question of agreeing upon the number of primitive segments belonging to the vagus, to enable us to locate with definiteness the hindermost limit of the head. Besides being of use in other ways, this would enable us to say, even in the earliest stages, what is head mesoblast and what is trunk mesoblast."[1]

I cannot see that Locy's determination of the limits of the cephalic plate helps us at all in the determination of the boundary of head and trunk. This boundary, as he states, has still to be determined. To fix the limits of head-mesoderm by a direct study of the mesoderm itself is quite as easy as to determine its boundary by the still hypothetical posterior boundary of the vagus region. According to Locy, the posterior limit of the cephalic plate separates neither what is pre-otic from what is post-otic, nor head from trunk.

My own observations on this point differ fundamentally from those of Locy, since according to my determination the line which separates the expanded cephalic plate from the region posterior to it marks the posterior boundary of the auditory invagination. This is of value, in so far as it enables us to distinguish those two regions — which on other grounds have always been held to be distinct — in stages earlier than was formerly possible. The posterior boundary of the cephalic plate is a clearly marked point at a stage before the neural folds begin to be raised dorsally, and it is situated just behind the region of greatest ventral flexure of the cephalic plate (marked by an arrow in Fig. 3, Plate **1**). This point may be traced into later stages, until the neural plate is transformed into a closed tube, when it is seen that it corresponds exactly with the hinder boundary of the hindbrain neuromere numbered VI in my figures (Locy's 10th "neural segment"); opposite this neuromere, as has been stated by many observers, lies in early stages the centre of the auditory invagination. The thickened auditory epithelium extends anterior and posterior to this neuromere; but it is opposite this neuromere that the first invagination to form an enclosed capsule takes place (see Plate **3**, Figs. 15 and 16). In later stages the ear capsule shifts backward, so that its centre comes to lie opposite the hindbrain neuromere numbered VII in my figures, which, as may be inferred from the statement above, lies in — or rather is afterwards differentiated from — the region behind the cephalic plate. I have been able to determine with certainty that the posterior limit of the cephalic plate

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[1] Locy finds that in later stages segments are added to the occipital region from the region of the trunk (see Tables I. and II.).

is a fixed one from a stage with seven somites, until the plate no longer exists as such. That it corresponds with the posterior boundary of neuromere VI of my figures, I am able to state with equal positiveness. Not having found, as Locy has done, eleven segments in the cephalic plate, by counting which one could determine the limits of the plate, I have been obliged to resort to other means. My method of determination has been as follows. As a fixed point in all the stages examined, I have taken the mesodermal somite marked 7 in Plates **1** to **4**. This, as I determine, is the most anterior somite which becomes innervated by a ventral spinal root; it therefore corresponds, I believe, with van Wijhe's 7th somite.[1] Anterior to this is formed a somite (van Wijhe's 6th), which in early stages possesses embryonic muscle fibres, but never becomes innervated by a motor root. Rabl ('92) said he could affirm with confidence that the somite (Urwirbel) which van Wijhe holds for the 6th or 7th head segment in an embryo with 48 somites is identical with that which he counts as the first trunk segment in an embryo of 76 somites. This mistake [?] of van Wijhe's, the accuracy of whose work in general is so well known, has led me to take especial pains to verify the identity of somite 7 in the stages most carefully examined, viz. from the stage with 6 to 7 somites, until after the neural tube is closed. Its identity has been determined as follows. I have carefully measured the distance from the constriction between van Wijhe's 2d and 3d somites — the mesodermic constriction which appears above the hyomandibular cleft — to the *partial* constriction anterior to van Wijhe's 6th somite. This distance measured in over two hundred embryos by means of camera-projection images, I have found to be practically constant, since it increases only very slightly as the embryo increases in length. Having thus determined the identity of this somite in successive stages, I have had a safe starting point for the determination of the posterior limit of the cephalic plate. I have measured the distance from the posterior cleft of van Wijhe's 7th somite, in the manner described above, to the posterior boundary of the widely expanded cephalic plate, and I have found this distance also to be constant. I chose to measure from the posterior boundary of van Wijhe's 7th somite, because by the measurement of this rather than a less distance the chances of error were diminished. The reader can verify the constancy of this distance by measuring the Figures (3 to 10) on Plates **1**, **2**, and **3**, which were drawn with the aid of a camera, and are magnified forty-three diameters. *This distance is almost precisely the same as the distance from*

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[1] Van Wijhe's 1e occipital Somit. Rabl's 3e distale Urwirbel.

the posterior boundary of somite 7 *to the posterior boundary of neuromere* VI, *after the closure of the neural tube* (see Figs. 7 and 10, Plate **3**, and Fig. 6, Plate **2**), and, as previously stated, the posterior boundary of the auditory invagination at first coincides with the posterior boundary of encephalomere VI. Again, and in direct confirmation of the evidence stated above, the posterior boundary of encephalomere VI is the posterior boundary of a greatly enlarged portion of the neural tube (Figs. 7–10, Plate **3**), as one would naturally expect, if it coincides with the posterior boundary of the previously widely expanded cephalic plate. With this fact in mind it is interesting to compare the conditions I have found with Locy's results. I believe he would not contest the assertion that my encephalomere VI is identical with his neuromere 10 (Zimmermann's encephalomere 11), because its relation to the ear vesicle at the time this is formed makes its identification a simple matter. Locy ('95, p. 522) says of the auditory vesicle: "When first established its centre occupies the space of the segment marked 10. Sometimes, in its earliest stages, the circular area spreads over the space of the three segments marked 9, 10, and 11, but I should say from my observations that, more frequently, it is not so widely expanded. It always settles down in Squalus acanthias to occupy the position first indicated, and subsequently it is shifted backwards." This accords with my identification of his segment 10 with my encephalomere VI, and this conclusion is corroborated by his statement that "the segment marked 8 is seated above a depressed region in which the first visceral cleft appears," for that is precisely the position of the encephalomere IV of my figures. On page 528, however, he says, "When the ear vesicle first arises it makes its appearance opposite the *ninth* neuromere" (!). Again, in his Figures 6 and 9, Plate XXIX., "neural segments," which are described (p. 528) as *8* and *9*, but which I believe to be segments *9* and *10* (as a comparison with my Fig. 46, Plate **7**, shows), are numbered *7* and *8* (!). Here, then, are three conflicts. Despite the elusive nature of Locy's "neural segments," I am disposed to regard his neural segment 10 (opposite which, as he has twice stated, the auditory invagination occurs) as identical in position with encephalomere VI of my figures. If this be true, there is no room on the cephalic plate for his neural segment marked 11, since, according to my determination, encephalomere VII is differentiated from the region of the neural tube which lies *behind* the broad cephalic plate, and does not become clearly marked off from the spinal cord region before a considerably later stage (stage H of Balfour). Therefore, if Locy's neural segment 11 is identical in position with my encephalomere VII, I see no escape from the conclusion that he has not "traced neural segments accurately up to the time they form neuromeres." It is hardly conceivable that he will bring forward in this instance the explanation previously offered in a similar case of mistaken identity, that somehow, between the stage with an open neural plate and a closed tube, segment 10 (neuromere VI) has *insidiously* come to assume the position previously occupied by his segment 11, and that segment 11 has been crowded backward. And it is likewise improbable that he would follow this explanation with another, — as he did in the case mentioned, — that encephalomere VI of my figures represents the "combined vesicle" of his segments marked 10 and 11.[1]

I now turn to the study of what I regard as the true primitive segmentation of the nervous system, — the so called neuromeric segmentation.

II. The "Hindbrain Neuromeres" in S. acanthias.

a. Definition of the Term "Neuromere."

In the preceding description the term "neural segment," or simply "segment," has been used as a non-committal term for structures of such different morphological value as those described by Locy under that name and the regular foldings of the neural tube. Locy ('95) has used the term "metamere" as synonymous apparently with his term "neural segment." Since, however, the term "metamere" is applicable by usage only to the successive similar parts of the body as a whole, it cannot be applied wisely to the successive parts of a single organ system, such as the nervous system.

Ahlborn ('84^a) was the first to use the term "neuromere," and he applied it to all the successive similar segments of the central nervous system. Béraneck ('84) applied the term "replis medullaires" and Kupffer ('86) the term "Medullarfalten" to the regular foldings seen in the brain region of Vertebrate embryos, those of the hindbrain being given by Béraneck the special appellation of "vrais replis." Since the

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[1] In a paper which comes to hand just as this goes to press, Locy ('97) states that he finds two sets of vesicles in the brain of chick embryos. Of these the first set, numbering seven in all, called by Locy "optic vesicles," are very ephemeral in existence, and have nothing whatsoever to do with the second set, called by him "brain vesicles." In Acanthias (Squalus) also he finds at least nine pairs of "optic vesicles," likewise very transitory. The exact relation of these to the "metameres" or "neuromeres" he does not state.

English equivalent of Kupffer's "Medullarfalten" and of Béraneck's "replis medullaires" (medullary folds) is used with an entirely different meaning from that intended by these writers, Orr ('87, p. 335) employed the term "neuromere" for the folds due to symmetrical constrictions seen in the hindbrain and the thalamencephalon, and distinctly stated that in Lizard embryos no neuromeres are found behind the vagus nerve. This limitation of Ahlborn's term has not, however, been accepted by later investigators. McClure ('89 and '90) again extended the term neuromere so as to include all the constrictions and dilatations of the neural tube, and classified neuromeres into: (1) *myelomeres,* due to constrictions of the myelon; (2) *encephalomeres,* resulting from constrictions of the encephalon. The latter term had, however, been previously used by Wilder ('89) for the large encephalic vesicles. Zimmermann ('91) adopted the term encephalomere, although he did not attempt to compare "Encephalomeren" with "Myelomeren," and Froriep ('94) used the term for theoretically homodynamous segments of the neural tube in the region of the head. He stated that the encephalomeres may correspond with neuromeres, but that this correspondence is not self-evident.

I shall adopt the nomenclature proposed by McClure ('89 and '90). In my account of the segmentation of the brain I shall begin with the conspicuous constrictions and enlargements of the hindbrain, which have uniformly been regarded by morphologists as typical neuromeres or encephalomeres. Orr's ('87) criteria for neuromeres, based on the study of the hindbrain of Lizard embryos, are as follows: (1) "Each neuromere is separated from its neighbors by an external dorso-ventral constriction, and opposite this an internal sharp dorso-ventral ridge, so that each neuromere (i. e. one lateral half of each) appears as a small arc of a circle." (2) "The constrictions are exactly opposite on each side of the brain." (3) "The elongated cells are placed radially to the inner curved surface of the neuromere." (4) "The nuclei are generally nearer the outer surface, and approach the inner surface only toward the apex of the ridge." (5) "On the line between the apex of the internal ridge and the pit of the external depression, the cells of adjoining neuromeres are crowded together, though the cells of one neuromere do not extend into another neuromere." Later investigations have served only to confirm this clear analysis of the structure of a neuromere.

b. DEVELOPMENT OF HINDBRAIN NEUROMERES.

Previous investigators have assumed that the hindbrain neuromeres possess the same characteristics at their first appearance that they do in later stages, whereas it will be shown in Squalus that this is not the case.

The want of abundant material of early stages felt by investigators in most cases is not a hindrance in the case of Squalus, for the early stages are as easily obtained as the later ones. In the study of the development of neuromeres, I have made use, first, of specimens very lightly stained in haematoxylin and mounted *in toto* in balsam, and secondly of the usual cross, frontal, and sagittal sections. The series of embryos represented in Plate **3** is chiefly of value in showing the neuromeres in successive stages, and the relations of the masses of cells composing the neural crest, or ganglionic Anlagen (colored blue in the figures), as seen in cleared specimens. The neural tube is represented as seen in optical section, while the other structures of the right half of the embryo are projected upon the median plane.

The earliest evidence of hindbrain neuromeres which I have found is seen in embryos of 14 or 15 somites in which the cephalic plate has not closed in the hindbrain region. In most embryos with that number of somites the plate is already closed, but in cases where it has not, neuromeres IV, V, and VI are seen as thickenings of the lateral walls of the hindbrain before its closure. Usually closure takes place, as in the chick, first in the region of the so called trigeminus Anlage, and later in the region of neuromere V, the most anterior portion of the cephalic plate remaining open as the neuropore until considerably later stages. Figure 7, Plate **3**, shows that in embryos of 14 to 16 somites (in the specimen figured, after the closure of the cephalic plate) four expansions of the neural tube in the hindbrain region are differentiated (neuromeres III, IV, V, VI). The hinder boundary of neuromere VI marks the former posterior boundary of the cephalic plate. The figures show (and this is a point of considerable importance in considering the morphological value of neuromeres) that each neuromere corresponds to the region of a dorsal as well as a ventral expansion of the neural tube, and that the neuromeres are separated from one another by both dorsal and ventral constrictions, which are to be seen both in sagittal sections and in cleared specimens.

Frontal sections at this stage give additional evidence concerning the structure of hindbrain neuromeres. A frontal section just below the axis of the neural tube is shown in Figure 22, Plate **5**. The section shows that the cephalic plate is still open in the region of the forebrain. The dorsal portion of the mesoderm in the region of van Wijhe's 2d and 3d head somites (2 and 3) is cut on the right side only, the sections not being exactly frontal on account of the torsion of the embryo. The lateral walls of the neural tube are seen in the figure to be thickened in that region which lies just posterior to the constriction opposite van Wijhe's 3d somite. A comparison of many frontal and sagittal sections leaves no doubt that this thickening lies in the region of neuromere IV. That expansion of the neural tube which lies between the 2d and 3d somites, and which is separated by an external constriction from neuromere IV behind and from the midbrain vesicle (encephalomere II of my figures) in front, is the most anterior of the primary expansions or encephalomeres of the hindbrain. It has been called by Zimmermann ('91) "Hinterhirn." This corresponds to the third expansion of the neural tube in the chick (Fig. 44, Plate **7**), as may be determined by its relation to the acustico-facialis Anlage and the auditory invagination. Failure correctly to identify this vesicle in the chick led Miss Platt ('89) to call the second vesicle, viz. the primary *midbrain*, the *hindbrain*.

At a later stage, when 17 to 18 somites are differentiated, a well marked local thickening in the posterior half of encephalomere III appears.[1] A frontal section of an embryo at this stage, showing neuromere IV as a local thickening posterior to neuromere III, is seen in Figure 23, Plate **5**. Encephalomere III is separated by a constriction from encephalomere II. At this stage, then, only four of the hindbrain neuromeres (III, IV, V, and VI) are differentiated, and the conditions remain the same when one more somite is formed.

In a similar frontal section of an embryo with 19 somites, such as is represented in Figure 24, four symmetrical thickenings of the lateral walls of the hindbrain (III–VI) appear. Opposite neuromere V lie the cells of the Anlage of the acustico-facialis nerve (blue), and opposite neuromere VI the thickened auditory epithelium. Neuromere VII is not present at this stage, and it does not begin to be differentiated until after one or two more mesodermal somites are formed, when a faintly marked dorsal and ventral dilatation appears in the region of the neural tube just behind neuromere VI (Fig. 9, Plate **3**). The lateral walls of this neuromere never become so markedly thickened as the walls of the other neuromeres, nor does the neuromere show a constriction at its posterior border before the embryo reaches the condition of Balfour's stage H, and then only a faintly discernible one. A cross section through neuromere IV, which serves to show how greatly thickened the lateral wall is at this stage, is shown in Figure 32, Plate **5**. The dorsal wall of this neuromere is considerably thicker than that of the neuromeres anterior and posterior to it, possibly because few cells are proliferated from this neuromere to form the ganglionic Anlage or neural crest.

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[1] Such a secondary subdivision of encephalomere III. ("Hinterhirn") occurs in the chick as in S. acanthias. I regard the primary vesicle as of different morphological value from that of its subdivisions, for reasons which will be made more apparent when the relations of the vesicles are studied.

I pass now to a description of the hindbrain neuromeres (encephalomeres) at a stage with 28 or 30 somites (Balfour's stage H). Since at this stage the neuromeres are clearly differentiated, and the thinning and expansion of the roof of the hindbrain have progressed very little, this is a most favorable stage for the study of the structural and histological peculiarities of the hindbrain neuromeres.[1] Figure 13, Plate **3**, represents a cleared specimen at this stage, and Figure 25, Plate **5**, a frontal section of the same. Opposite neuromere III (Fig. 25) lies part of the trigeminus Anlage ; opposite neuromere V lie the cells of the acustico-facialis Anlage ; and opposite neuromere VI lies the thickened auditory epithelium, which is just beginning to invaginate. The acustico-facialis Anlage always remains in relation with neuromere V, so that this serves as an excellent starting point in counting the neuromeres. In order to get a clear conception of the structure of the neuromeres, cross, frontal, and sagittal sections are necessary. The series represented in Figures 36–38, Plate **6**, are frontal sections taken at different levels (α, β, γ, Fig. 40, Plate **6**) in the medullary tube. Only the right wall of the medullary tube in the region of neuromeres IV and V is shown in detail. The first section (Fig. 36) is dorsal, in the region of the "Deckplatte." In this section it is seen that what Orr ('87) has said for the Lizard (see page 167) is true for Squalus. The section reproduced in Figure 37, more ventral than Figure 36, shows that the conditions which obtain in the region of the lateral zones are somewhat different from those of the dorsal zone. Since no sharp internal ridge exists, each lateral half of a neuromere does not appear in section as an arc of a circle, but as a thickening of the wall of the medullary tube. The cells and nuclei are fewer in number and more crowded in the region of constriction between neuromeres. Although there is no inner concavity at this level, the cells and nuclei (Fig. 37) show a radial arrangement similar to that shown in Figure 36. The ventral section (Fig. 38) differs in no essential respect from the dorsal one. I have chosen these two neuromeres (IV and V) for description, since they with neuromere VI show the characteristics stated above in the most marked way. Only a faint external constriction, without internal constriction or ridge, separates neuromere VII from the region of the spinal cord.

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[1] The head somites, likewise, appear at this stage most clearly differentiated. It is, in fact, the "acranial stage" of the embryo.

At a stage with fifty somites (Balfour's stage K) the structure of the neuromeres is slightly but not materially changed. In Figure 17, Plate **3**, is represented an embryo of this stage, viewed as a transparent object. Figures 26–29, Plate **5**, show four frontal sections of such an embryo, Figure 26 being the most dorsal, and Figure 29 the most ventral of the series. Figure 26 shows that the most dorsal portion of the Deckplatte has become very thin, being only one layer of cells thick. The constrictions and dilatations are only faintly shown, the nuclear arrangement being the same in the region of the constriction as in the region of dilatation. Figure 27, more ventral than Figure 26, though still in the region of the Deckplatte, shows the conditions, both nuclear and cellular, to be almost precisely the same as in Figure 36, Plate **6**. The internal ridges, or cusps, are sharp, and the cells in the region between the internal ridge and external constriction are closely crowded together. It is to be noted that the separation of the lateral walls of the hindbrain is least marked in the region of neuromere VI, opposite which the ear capsule lies (compare Fig. 17, Plate **3**). Figure 28 seems to show that the neural walls have become considerably thickened in the region of the lateral zones. There is no doubt that the lateral zones are absolutely and relatively thicker than at the stage last described, while the neuromeres have increased in length. It is to be observed that this thickening is accompanied by a change in the outline of the lumen of the tube, vertical grooves appearing in the place of the vertical ridges of the more dorsal sections. In the most ventral of the sections, Figure 29, the internal ridges appear again, though the concavity of the inner surface of each neuromere in the antero-posterior direction is only faintly indicated.

During stage K, as the result of the great expansion and thinning of the Deckplatte in the region of the medulla oblongata, the neuromeres come to affect only the lateral zones. Locy ('95, pp. 524 and 525) notes changes in the appearance of the "neural segments" at this stage, the explanation of which he does not state with precision. His opinion seems to be, however, that a union of part of each of the original segments with the segment lying just in front of it, accounts for this condition. An examination of the series of Figures 7 to 21 of my Plates **3** and **4**, and of the frontal sections of Plate **5**, shows that no such fusion of neuromeres takes place. The constrictions and ridges between neuromeres never shift their position, the only change being a gradual assumption, by each of the local thickenings, of an inner concavity in the region of the lateral zones.

Frontal sections of an embryo 15 mm. long show that dorsally all traces of the neuromeres are lost. A frontal section in the region of the lateral zones from an embryo of this stage is represented in Figure 30, Plate **5**. A great separation of the lateral walls of the medulla is seen to have taken place in the region of neuromeres III, IV, and V. At this stage only do the neuromeres possess the characteristics described by Orr for the Lizard (see page 167). While the external constrictions are only faintly shown, owing to the increase of the "white substance" on the sides of the medulla, the internal ridges and concavities are well marked. From this stage onward the neuromeres begin to disappear. In embryos of 40 mm. to 50 mm., neuromere VI, in relation with the facialis nerve, is the most clearly marked of the neuromeres.

Before passing to an examination of the evidence of neuromeres in the trunk region, I wish to emphasize the fact that the hindbrain neuromeres cannot be regarded as structures dependent upon the pressure of mesodermal somites. Being local thickenings of the lateral wall of the neural tube they are obviously inexplicable on such a simple mechanical basis. They are structural differentiations of the tube in regions where the mesoderm has not yet extended, — that is, in the dorsal and lateral portions of the tube, the mesoderm of the head being still ventral in relation to the neural tube.

c. SUMMARY.

In the preceding study of the hindbrain neuromeres in S. acanthias, I have supplemented Orr's criteria (applicable to later stages) by a description of the structure of the neuromeres in Squalus in earlier stages of development, i. e. in embryos of 14–50 somites. The characteristics possessed by hindbrain neuromeres in these earlier stages may be summarized as follows. Each neuromere is separated from its neighbor by an external constriction, which passes entirely around the neural tube. There is dorsally and ventrally an internal ridge corresponding to this external constriction; but the ridge vanishes in the region of the lateral zones, being replaced by an internal depression or groove. The nuclei of the lateral wall are, however, still arranged (Fig. 37) in a manner which approximates that of the region of the internal ridges, notwithstanding that the thickening of the lateral wall of the neuromere has actually obliterated all surface evidence of such a condition. Each hindbrain neuromere, therefore, consists of a lateral thickening and a dorsal and ventral dilatation of the wall of the neural tube. The constrictions are exactly opposite on the two sides of the brain. The elongated cells are placed radially to an imaginary point situated in the middle of the thickening of the wall opposite. The nuclei are generally nearer the outer than the inner surface, and approach the latter only in the region of the constriction between the neuromeres. In this region the cells are more crowded, but the cells of one neuromere do not extend into the adjacent neuromeres.

The hindbrain neuromeres, being structural differentiations of the walls of the neural tube, are not to be explained as the result of a simple mechanical process. The essential similarity of these serial groupings of nerve cells to the metameric ganglia of Annelids will, I believe, impress others as well as myself. A reconstruction of the neuromeres as they appear in this typical condition is shown in Figure 40, Plate 6.

III. The Neuromeres in the Trunk Region.

a. DEVELOPMENT OF MYELOMERES.

It might seem that a more natural sequence in the study of neuromeres than the one here followed would be to pass from the simpler conditions which obtain in the trunk to the more complicated ones in the head region. Instead of this, I follow the historical sequence, having begun with the "Kräuselungen," or foldings, first seen by observers in the region of the hindbrain, and now pass to the study of the conditions in the spinal cord. That "hindbrain neuromeres" could be compared with segments of the spinal cord was an afterthought on the part of embryologists, evidently born of the conception that the head has a segmentation comparable with that in the trunk.

While the neural plate in the trunk region is still widely open, its dorsal surface exhibits cross furrows, which are proved by longitudinal sections to correspond with the interspaces, or clefts, between the mesodermic somites. The number of the cross furrows exactly equals that of the interspaces, increasing in number as the constrictions between the somites do. They do not, however, extend to the edges of the neural plate, but are restricted to the region where the plate rests upon the somites. In these cross furrows we have the first indications of those structures which were called by McClure ('89) "myelomeres," and were compared by him with the "neuromeres" of the medulla.[1] Such symmetrical cross furrows on the widely expanded neural plate of embryos of Salamandra atra were described by Kupffer ('86), and considered by him as remnants of a primitive segmentation. Since Kupffer believed that at this stage there was no trace of mesodermic somites, he regarded the segments as "primary," i. e. not formed secondarily in adaptation to the mesodermal segmentation. Both Froriep ('92) and Wiedersheim ('92) have, however, declared that mesodermal somites are present at the stage described by Kupffer, and that the segments could be explained as the passive result of the pressure of these somites. Locy ('95) finds in the trunk region of embryos of S. acanthias with a widely expanded cephalic plate that the lines of division between his "neural segments" may be traced inward toward the median furrow, probably as the result of the appearance of somites in that region. As stated on page 160, I have failed to find this exact correspondence between the neural segments of Locy and the somites.

When the neural plate has closed to form the neural tube, the regions of elevation between the furrows become constrictions, which however affect only the ventral half of the tube, i. e. that portion against which the somites lie (see Fig. 41, Plate **6**). Neither frontal sections nor cleared specimens give evidence of constrictions in the dorsal half of the tube. The constrictions in the ventral half of the tube are most clearly marked in the early stages, when the mesodermal somites are most rounded in form, and they disappear as this rounded form disappears.[2]

Figure 39, Plate **6**, represents a frontal section in the ventral half of the myelon of an embryo with 28–30 somites (Balfour's stage H). The right half of the neural tube and of the mesoderm is shown. It is seen that the wall of the neural tube shows a rounded constriction opposite the somite, while opposite the cleft between two somites, and conforming with it, an outer ridge and an inner rather sharp groove are seen. This section affords evidence more favorable to the contention that "neuromeres" exist in the spinal cord than that seen at any other stage of development, or in any other plane of sectioning. In dorsal sections of the same series the constrictions disappear, as do the somites also.

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[1] Marshall ('78) had previously stated that in the chick "the cord is slightly constricted opposite the centres of the protovertebræ, and slightly dilated opposite the intervals between successive protovertebræ."

[2] Miss Platt ('89) has said with regard to the chick, "Here [in the trunk region] as in the medulla, the segmentation is more manifest in the ventral region than in the dorsal."

The structure of the myelomeres in embryos of 40–50 somites is represented in Figures 42 and 43, Plate **6**. As in Figure 39, only the right half of the embryo is shown. The only evidence of the structural peculiarities of neuromeres at this stage consists in an external constriction opposite the myotome and the spinal ganglion (Fig. 43). In sections dorsal or ventral to the one shown in Figure 43, even this constriction becomes lost (see Fig. 42, which is more ventral, occupying the region of the ventral roots). All traces of an internal dilatation and constriction, and of the concomitant radial arrangement of cells, have disappeared. In the head, on the contrary, the "neuromeres" still preserve all the characteristics seen in the earlier stages.

An examination of the structure of the myelomeres shows that the conditions are easily explicable on the mechanical grounds stated. There are no serial thickenings of the wall of the neural tube, as in the hindbrain, and the radial arrangement of cells and nuclei shown in the frontal sections (Fig. 39) presents no difficulty; for the cells composing the epithelium of the neural tube always have their long axes perpendicular to the surface of the tube, so that, if the tube becomes constricted opposite each somite, the cells will necessarily show a radial arrangement in frontal sections. In view of this fact, it is difficult to understand how investigators should have thought that the existence of a radial arrangement of cells and nuclei was evidence sufficient to establish the morphological value of myelomeres, and their serial homology with hindbrain neuromeres. McClure ('90), for example, says, "The lateral walls of the spinal cord are divided into neuromeres which, while less conspicuous, have all the cellular characteristics seen in the typical neuromeres of the hindbrain, and in fact are a continuation of the latter." That all of the cellular characteristics seen in the typical neuromeres of the hindbrain are also found in the myelomeres is demonstrably untrue for Squalus, as may be seen by comparing the sections shown in Figures 38 and 39, Plate **6**, both from the ventral half of the neural tube of the same embryo, one in the head and the other in the trunk. The cellular arrangements are decidedly unlike. In the head (Fig. 38) the cells and nuclei are crowded in the region of constriction between neuromeres, while in the trunk, if the cells are crowded at all, it is in the region of dilatation of the myelomere.

It has seemed a strong argument for the serial homology of myelomeres and hindbrain neuromeres that the former continue into the latter gradually and in an unbroken series. For example, McClure ('90) stated that "the constrictions of the myelon (in Lizard embryos) gradually pass or merge into those of the encephalon, thereby forming a continuous series of constrictions throughout the entire length of the neuron, which increase in size anteriorly." Also, in demonstrations of this continuity, Miss Platt ('89) stated (for the chick) that "the difference (in size) between the fifth neuromere [last neuromere of the medulla] and the next posterior fold is not as great as the difference between the second and third neuromeres." (Compare Fig. 44, Plate **7**.) Locy ('94 and '95) says of his neural segments that "those in the trunk region are continuous with those of the head, and pass into the latter without any transition forms." Zimmermann ('91), on the other hand, does not find the spinal cord in S. acanthias to be segmented.

While I am able to confirm the evidence of continuity of encephalomeres and myelomeres as stated by previous investigators, I am unwilling on this ground alone to regard these structures as of the same morphological value. Moreover, it has been shown that the hindbrain neuromeres and the myelomeres differ both in structure and in development.

b. Summary.

The evidence presented by the constrictions of the myelon warrants the inference that the existence of the myelomeres is dependent upon the presence of the somites, an explanation by no means possible for the hindbrain neuromeres. The constrictions of the myelon appear only after the somites are formed, and increase in number with the addition of new somites. They are opposite the somites, and are confined to that portion of the neural tube against which the somites lie, i. e. the ventral portion. They present no histological or structural conditions which are not easily reconcilable with the hypothesis of their mechanical formation. In those Vertebrates in which the somites extend farther dorsally with reference to the neural tube, the constrictions of the myelon also have a greater dorsal extent. As soon as the somites lose their rounded form and no longer lie close to the neural tube, the constrictions of the tube disappear. As a whole, the evidence in the spinal region of Squalus fully confirms the explanation given by Minot ('92), viz. that the appearance of the myelomeric constrictions "seems to depend upon the development of the primitive segments of the mesothelium. When the segments are fully formed, and before their inner wall has changed into mesenchymal tissue, they press against the medullary tube and oppose its enlargement; at least one sees that the tube becomes slightly constricted between each pair of segments and slightly enlarged opposite each intersegmental space." Structurally, therefore, myelomeres and encephalomeres differ. While a mechanical explanation is possible for the one, such is not possible for the other. They are, it is true, continuous serial dilatations of the neural tube. The proof, however, that they are of equal morphological value, that is to say, serially homologous, rests, I believe, in the demonstration of a similar metameric relation to organs known to be segmental. The myelomeres correspond metamerically with the somites, as has been stated. Do the encephalomeres likewise correspond with somites? Upon the answer to this question obviously depends largely the decision as to their *metameric* value. Before stating the evidence bearing upon this question it is necessary to see if there is any evidence of neuromeres anterior to the hindbrain.

IV. The Neuromeres anterior to the Hindbrain.

a. ESSENTIAL CRITERIA OF NEUROMERES.

I believe that those who find neuromeres in the brain region anterior to the hindbrain have assumed the presence of a homodynamous segmentation of the entire encephalon. Yet it must be admitted that even if a serially homologous segmentation extends from the spinal cord into the medulla oblongata, it by no means follows that such segmentation also extends into the anterior brain region. Compare with the analogous case of the skull. Because the occipital region is segmental, i. e. composed of fused vertebræ, it does not follow that the pre-otic region is. It is well, at least, to study the conditions in the anterior brain region with the mind as unprejudiced by any theory as possible. What criteria, then, warrant the conclusion that any given division of the neural tube is a neuromere? Certainly, no one criterion would be held to be sufficient. The best criteria are such as associate the supposed neuromeres metamerically with other structures known to be segmental, e. g. the mesodermic somites or the segmental nerves. But where such direct evidence is wanting, to say that a radial arrangement of cells and nuclei is evidence of a neuromere, and thus indirectly evidence of a metamere, is obviously dangerous, since the radial arrangement of the nuclei appears whenever the neural tube is constricted from any cause whatever.

If, however, we have rudimentary somites in the head, may we not also have rudimentary neuromeres? McClure ('89) finds between the midbrain and the optic vesicle of the Lizard a structure which resembles a portion of a neuromere, — a "half-neuromere." He accepts the evidence of neuromeres in the primary forebrain also, although the arrangement of nuclei does not always conform to the typical condition. Waters ('91, p. 143) says: "In this area [that of the posterior commissure] the Cod brain shows little or no segmentation, but from the fact that it nearly corresponds in extent to neuromere II, and that its existence is quite evident in Amblystoma, it seems probable that this space is occupied by the third and last of the forebrain neuromeres." In other words, though none of the characteristics of a neuromere are present, it is *a priori* probable that a neuromere exists here!

Orr, Béraneck, and Miss Platt have regarded the midbrain vesicle as a single enlarged neuromere. It has an external constriction separating it from its neighbours, a corresponding internal ridge, an inner concavity, an outer convexity, a radial arrangement of cells and nuclei, and in addition is primary in time of appearance. On the other hand, Waters ('92) says that it is an error to confound the neuromeric segmentation with the so called vesicular segmentation, since he finds in the midbrain region "*two*[1] well marked convolutions of the brain wall," and the characteristic radial arrangement of nuclei. Kupffer ('93^a) believes that, since, with Froriep (92^a) and Zimmermann (91), he finds evidence of *three* encephalomeres in the midbrain,[2] this confirmation gives a certainty to their results.

Surely the divergence in the results of other investigators has not *proved* that Orr, Béraneck, and Miss Platt were wrong in considering the primary midbrain as a single neuromere, especially since the midbrain and forebrain form parts of a continuous series of primary enlargements of the encephalon. The majority of investigators (Orr, Béraneck, McClure, Froriep, and Zimmermann) find that the forebrain consists of *two* neuromeres, without however giving a satisfactory explanation of its marked divergence, in the matter of secondary division, from the typical hindbrain dilatations. If we count dorsal expansions, as is done by Waters and others, we may find evidence of at least *three* neuromeres, which correspond, says Kupffer ('93^a), with his Grosshirn, Nebenhirn, and Schalthirn. Furthermore, if dorsal diverticula be regarded as evidence of neuromeres, we must agree with Kupffer that it is impossible to disregard the epiphyses and plexus formations.[3] On this basis

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[1] Waters says (p. 465) that he thinks McClure is mistaken in assigning to the midbrain region, on purely speculative grounds, a *third* neuromere.

[2] Kupffer found these three secondary subdivisions of the midbrain in Cyclostomes, Zimmermann in Selachii, and Froriep in Mammalia.

[3] See Kupffer ('93^a, p. 549).

Kupffer finds at least *five* encephalomeres in the primary forebrain. This conclusion seems strengthened by the conclusion of Burckhardt ('93), that the median zones of the neural tube retain throughout the Vertebrate series the primitive segmentation best, and therefore are the best for comparison.

My conclusions from a study of the evidence presented by those who have assumed a segmental value for the secondary subdivisions of the forebrain and midbrain vesicles are, (1) that morphologically different structures have been described by them as "neuromeres" or "encephalomeres," and (2) that the divergence in their results does not seem to justify this assumption.

I now turn to an examination of the development of forebrain and midbrain regions in S. acanthias, in order to determine whether or not it is probable that structures morphologically comparable with hindbrain neuromeres exist in these regions. Since hindbrain neuromeres involve all three zones — dorsal, ventral, and lateral — of the walls of the encephalon, the value of forebrain and midbrain segments as morphological equivalents of them will clearly depend on their similarly involving those zones. If they do not, it is incumbent upon one who holds to their equivalency to demonstrate how modification has probably obscured or obliterated the primitive conditions. Evidence in such a highly specialized region can be at best only probable. Here, however, as always, the demonstration of morphological comparability must be "controlled" by the demonstration of similar relationships to other organ systems.

b. DEVELOPMENT OF THE FOREBRAIN AND MIDBRAIN.

At a stage with 19 or 20 somites the conditions in the anterior brain region are very simple. The primary forebrain and midbrain are simple vesicles or enlargements of the neural tube. A parasagittal section cut through the right wall of the neural tube is represented in Figure 45, Plate **7**. Six vesicles are counted, all of them being included in the region of the cephalic plate. The anterior vesicle shown is the wall of the forebrain in the region of the optic vesicles. Behind lies the midbrain, separated by a slight constriction from that region of the hindbrain to which Zimmermann ('91) has given the name "Hinterhirn."[1] Hindbrain neuromeres IV, V, and VI are clearly defined.

A frontal section of an embryo of the same stage, so cut as to coincide with the axis of the midbrain vesicle, is shown in Figure 49, Plate **7**. The vesicle of the primary forebrain (I) appears as an almost circular enlargement of the anterior portion of the neural tube. Behind this, and separated from it by a constriction, lies the narrower and somewhat more elongated midbrain vesicle (II). Posteriorly a small portion of the "Hinterhirn" vesicle also appears in the section.

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[1] The English term hindbrain has been applied to the region separated by the Germans into "Hinterhirn" and "Nachhirn."

Sagittal sections of embryos at this stage are seen in Figures 8 and 9, Plate **3**. Faint dorsal constrictions separate forebrain, midbrain, and "Hinterhirn" (III), the separation between midbrain and "Hinterhirn" being very slight. A deep depression in the floor of the forebrain marks the position of the infundibulum, which is bounded posteriorly by a faint constriction, the first indication of the tuberculum posterius (Kupffer). Another constriction of the ventral wall of the neural tube is seen behind the tuberculum posterius in the region of the midbrain, — the plica encephali ventralis. In later stages the region of this constriction becomes the point of greatest flexure of the neural tube. The constrictions marking off the brain vesicles appear as rather broad depressions, not sharply defined as are the constrictions between neuromeres. The brain vesicles are also seen to be considerably larger than the hindbrain neuromeres, the difference in size constantly increasing from this stage onwards. Except for a local thickening of the lateral zones, the two anterior brain vesicles are structurally quite comparable with the hindbrain neuromeres. They similarly involve all three zones of the neural tube.

An examination of embryos at a stage with 28 to 30 somites, i. e. early in Balfour's stage H, shows that slight changes have occurred. A parasagittal section of such an embryo is shown in Figure 46, Plate **7**. The anterior vesicle, the forebrain, is so cut that one sees its lumen. Behind this, and separated from it by a constriction which extends to the ventral portion of the tube, lies the midbrain, which dorsally is a single expansion passing almost without constriction into the hindbrain. The depth of the constriction is much less than it appears to be in this figure, because the section passes to one side of the median plane. In the ventral half of the midbrain there is a constriction, which more median sections of this stage (Fig. 13, Plate **3**) show to correspond with the region of sharpest flexure of the neural tube (plica encephali ventralis). This constriction does not extend, however, to the dorsal portion of the neural tube, and therefore is not equivalent to a constriction which separates neuromeres. By it the midbrain is separated ventrally into two lateral expansions on each side of the head, — one anterior, the other posterior, — while dorsally it remains a single dilatation. The anterior of the two expansions narrows as it extends ventrally, and terminates at a point in the ventral wall near, but anterior to, the tuberculum posterius. The posterior of the two midbrain expansions is bounded behind by the faint lateral constriction between midbrain and hindbrain vesicles.

The conditions shown in a sagittal section at this stage are not essentially different from those presented at the stage previously described (Fig. 13, Plate **3**). The forebrain, midbrain, and "Hinterhirn" vesicles are separated by very faint dorsal constrictions. In the constriction between forebrain and midbrain vesicles appears later Miss Platt's "thalamic nerve." Ventrally two constrictions are seen, one corresponding with the tuberculum posterius, and the other, more posterior, with the point of greatest flexure of the neural tube. Two frontal sections of an embryo at this stage are shown in Plate **7**, Figures 48 and 50. Figure 48 represents the more dorsal of the two, and shows only the expansion of forebrain and midbrain vesicles separated by the primary constrictions spoken of above. A small portion of the "Hinterhirn" is shown. The section shown in Figure 50 is more ventral, being in a plane about midway between the dorsal and ventral sides of the neural tube. An arrow is drawn at the constriction separating forebrain and midbrain vesicles. This constriction corresponds with the one seen in the more dorsal section, also indicated by an arrow. Behind this, in the region of the midbrain, another constriction appears, one which was not seen in the dorsal section. This may be traced in more ventral sections into the constriction previously described as occupying the floor of the midbrain at a point corresponding with the point of greatest flexure of the neural tube. In my opinion everything in front of the arrow belongs to the primary forebrain, the lateral walls of which are expanded to form the optic vesicles. Behind these two vesicles are seen "two well marked constrictions and two convolutions" of the neural wall which show radially arranged nuclei.[1] It is found in later stages that the posterior of the two constrictions corresponds in position with the posterior commissure, and therefore that what lies anterior to this constriction must be considered as part of the thalamencephalon. It is seen, therefore, that the constriction between primary forebrain and midbrain vesicles does *not* correspond with the posterior commissure, which in later stages forms by common consent the anterior boundary of the midbrain (see

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[1] Probably the two "neuromeres" of the thalamencephalon described by Orr ('87).

Plate **7**, Fig. 47, *coms. p.*). This constriction corresponds, instead, with a point just behind the epiphysis, and is separated from the posterior commissure by that portion of the brain which Kupffer has named Schalthirn, or diencephalon (the Schaltstück of Burckhardt). Neither of the so called neuromeres (Orr) is in relation with a nerve, motor, or sensor, and neither possesses a dorsal expansion of its own.

A parasagittal section of the next older stage represented is seen in Figure 47, Plate **7** (compare Fig. 19, Plate **4**); it is of an embryo with 65 somites (Balfour's stage K), and the changes in the anterior brain region are seen to be considerable. In the dorsal portion of the region called primary forebrain, i. e. the region anterior to the constriction in which the "thalamic nerve" (*thl.*, Fig. 18, Plate **4**) lies, two expansions now appear. These are median, unpaired, and separated from each other by a constriction which extends toward, but does not reach, the optic stalk. The anterior expansion is the prosencephalon (Grosshirn, epencephalon of Kupffer), which involves, as determined by His (88^b), the "Deckplatte" and both "Flügelplatten." The second, which at this stage is a simple expansion, later becomes differentiated into "Zirbelpolster" (Kupffer's parencephalon, Nebenhirn) and the epiphysis. The latter, according to His, is derived from the "Deckplatte" only. The primary constriction between forebrain and midbrain is marked in Figure 47 by the dorso-ventral line, behind the second expansion. The midbrain now shows three lateral expansions. The anterior is bounded in front by the primary constriction between forebrain and midbrain, and behind, as in the previous stage, by the ventral (and now lateral) constriction which extends dorsad toward the posterior commissure from a point just in front of the chief root of the oculomotor nerve. The second dilatation has as its posterior boundary a ventral constriction which I do not consider of morphological importance, because it simply corresponds with a point of flexure of the ventral wall of the tube, never extends to a dorsal position, and has no corresponding inner ridge. The constriction exists, however, at this stage, and forms the posterior boundary of a neural segment related to the oculomotor nerve. Behind this lies a third expansion, faintly marked anteriorly and also posteriorly, where it merges into the isthmus. In later stages the trochlear nerve arises from the region of the posterior constriction of this expansion; it is the chiasma of fibres of this nerve which defines the posterior constriction of the midbrain vesicle. In this stage, as in the preceding, the midbrain vesicle remains dorsally a simple expansion, the constrictions affecting only its lateral and ventral walls.

Two frontal sections of an embryo at this stage are seen in Figures 51 and 52, Plate **7**. Anteriorly in the more dorsal section (Fig. 51) is seen the expansion of the prosencephalon. Behind this lies an expansion which might be considered as a neuromere, if a radial arrangement of nuclei and a constriction of the brain wall were alone considered sufficient criteria for such a structure. Since, however, it is simply a dorsal expansion, which is unrelated to nerves, and soon becomes differentiated into adult organs, I am unable to regard it as a neuromere. From it are differentiated "Zirbelpolster" (parencephalon, Nebenhirn, or Zwischenhirnblase) and epiphysis. Posterior to the constriction marked by the arrow, which corresponds with the point so marked in Figure 50, is situated a long expanded portion of the encephalon which passes without constriction into the midbrain vesicle. In the more ventral section (Fig. 52), however, there is seen in this region a constriction which may be traced ventrally to that point from which the anterior root of the oculomotor arises. Two neuromere-like expansions, separated by the constriction between primary forebrain and midbrain, are seen in this stage as in the previous stage described.

Passing now to a much later stage (21–22 mm.), we find (Plate **4**, Fig. 21) that the posterior commissure has come to lie much nearer the base of the stalk of the epiphysis, and thus that the portion of the dorsal wall which is called by Kupffer diencephalon has become much reduced in the region of the midbrain vesicle. Thus it has come about that frontal sections in a plane midway between the dorsal and the ventral walls of the neural tube (Fig. 53, Plate **7**) show only a single neuromere-like expansion. In more dorsal as well as more ventral sections this undergoes constriction, so that it is by no means a simple neuromeric enlargement. A median sagittal section, such as that shown in Figure 21 (Plate **4**), is the most satisfactory for the study of segmentation at this stage. The primary forebrain is now differentiated into the successive dorsal dilatations epencephalon, paraphysis (parencephalon), and epiphysis. Dorsally the midbrain still continues to be a simple expansion, while ventrally traces of the three segments still remain, the anterior one having become much reduced in length.

With the exception of Locy, Zimmermann ('91) is the only investigator who has studied the "neuromeres" in Selachii. For the purpose of comparison, it is well to state his results here. He finds at first *eight* "primäre Abschnitte" in the encephalon, the first three of which exceed in size the last five. The first three are the Vorderhirn, Mittelhirn, and Hinterhirn, each of which he regards as a complex of encephalomeres, since they later subdivide into segments which dorsally are equally long and broad. The Vorderhirn divides into two encephalomeres, the Mittelhirn into three, and the Hinterhirn into three. Thus, since the posterior five "primäre Abschnitte" do not further subdivide there are in all thirteen "encephalomeres." As a result of cephalic flexure some of the encephalomeres become wedge-shaped, but all are clearly separated from one another by constrictions. Zimmermann's paper was a preliminary one without figures, and it has not as yet been followed by a final paper.

It is seen that Zimmermann's account, based on the study of S. acanthias embryos, differs somewhat from my own. At the closure of the neural tube I find six vesicles or expansions of the encephalon. The first three correspond with those called by Zimmermann Vorderhirn, Mittelhirn, and Hinterhirn; the last three are hindbrain neuromeres IV, V, and VI. Since Zimmermann's 7th and 8th "primäre Abschnitte" are not differentiated at this stage, I am unable to accept his conclusion that there are at first *eight* primary "encephalomeres" or "Abschnitte." The primary forebrain subdivides into the two dorsal expansions which Zimmermann calls "Secundäre Vorderhirn" and "Zwischenhirn." But, if these are "encephalomeres," I am unable to see how later differentiations, such as the prosencephalon (epencephalon), paraphysis (parencephalon), and epiphysis can be excluded from the same category. May we not have tertiary as well secondary "encephalomeres"? I am unable to accept Zimmermann's single criterion of size as sufficient to enable us to make a distinction between those segments which are primitive, i. e. remnants of ancestral structures, and those which are the early beginning of adult organs. A most serious objection to regarding such structures as Zimmermann's "Secundäre Vorderhirn" and "Zwischenhirn" morphologically comparable with neuromeres or myelomeres has been stated by Herrick ('92), and consists in the difficulty of homologizing dorsal expansions with ventral ones.

The primary midbrain, as stated by Zimmermann, subdivides into three segments, the most anterior of which lies in front of the posterior commissure and in front of the place of origin of the oculomotor nerve. In all stages the midbrain is seen in median sagittal sections to present a simple dorsal expansion, its constrictions affecting its ventral and lateral walls only.

The third vesicle, Zimmermann's Hinterhirn, which he says subdivides into three "Encephalomeren," I find to become differentiated into the cerebellum Anlage and a posterior enlargement or thickening, but nothing more. The only evidence which I find of Zimmermann's anterior "Hinterhirn Encephalomer" consists of a flexure of the median ventral wall appearing in late stages in the anterior portion of the Hinterhirn. Since no dorsal or lateral constriction corresponds with this, and since therefore it cannot be regarded as a vesiculation of the neural tube, I do not consider it as of morphological importance, but explicable simply as a passive result of the flexure of the neural tube.

Locy ('95, p. 542) finds five "neural segments" in the forebrain and midbrain, — three in the former and two in the latter. He clearly figures and mentions in the description of plates, however, the three secondary midbrain expansions described by Zimmermann and myself.

c. SUMMARY.

An examination of the literature bearing on the question of neuromeres in the region anterior to the hindbrain had led me to the conclusion that structures of different morphological value had been described as neuromeres, and the examination of the secondary subdivisions of the forebrain and midbrain of embryos of S. acanthias has served to strengthen this opinion. These subdivisions have been shown to differ from the typical neuromeres in shape, in structure, and in relation to the dorsal and ventral zones of the neural tube. The attempt to establish a serial homology on the basis of such structures alone seems to me quite misleading; not less so, indeed, when we attach hypothetical nerves (dorsal, lateral, and ventral roots) to them.

Moreover, the late appearance of the so called neuromeres of the anterior brain region, together with the fact that they are secondary subdivisions of primary vesicles, and thus differ from the hindbrain and spinal expansions, seems a serious objection to the contention that they afford satisfactory evidence of a primitive metamerism. Zimmermann ('91) attempted no explanation of this difficulty, saying merely that the differentiation of the anterior encephalomeres *is retarded* for reasons unknown to him. Waters ('92) alone offers an explanation. To him it seemed "not unreasonable to conjecture that these constrictions, being essentially primitive and in a state of degeneration, have gradually been more and more crowded out by the specializing brain development, and hence appear at a much later period in the ontogeny than would be expected." What right, we are tempted to ask, has one to *assume* the primitive nature of "forebrain neuromeres," in view of the *facts* that they are late differentiations, and that some of them are the fundaments of adult organs, and in this respect differ both from the typical hindbrain neuromeres and from the expansions of the myelon? Every fact which we possess seems to me to argue against their primitive nature. In my opinion the assumption of Herrick ('92), that, "if neuromeres once existed in the forebrain, they would be visible only at an early stage, and would be obscured by altered conditions," is the more reasonable of the two assumptions. On the basis of structure and of relation to other segmentally arranged organs, however, I conclude that the primary vesicles, the forebrain and midbrain, give evidence — as do the primary expansions of the hindbrain — of the primitive segmentation of the Vertebrate head. I now turn to an examination of these relations, first, to those of neuromeres and somites, since they are the most important.

V. The Relation of Neuromeres to Somites.

a. Relation of Myelomeres to Somites.

Since the myelomeres, as has been stated, show a definite (numerical) correspondence with the trunk somites, the expansions of the spinal cord alternating with the somites, it is evident that proof of the serial homology of myelomeres and encephalomeres will rest very largely on the demonstration of a similar correspondence of the latter with head somites, if there be such. Yet, so far as I know, Miss Platt is the only investigator who has affirmed that there is such correspondence for the head region. She writes ('91, p. 82) as follows: "The line of somites [in Squalus] alternating with the neuromeres is continued into the head as far forwards as the alimentary pocket which is to form the second visceral cleft. Here complete divisions of the mesoderm cease, but serial depressions in its dorsal wall indicate incomplete divisions into three parts above the hyoid arch (van Wijhe found *two* somites here) and two parts above the mandibular arch [van Wijhe found *one* somite here]. Like the somites of the trunk, the divisions thus marked off alternate with the neuromeres, lying opposite successive constrictions of the brain. The anterior division of the mandibular cavity corresponds to the constriction that separates the midbrain from the hindbrain, or to that from which the trochlear nerve arises." The same investigator likewise says in regard to Necturus ('94, pp. 960, 961): "Hinter der Hyomandibularspalte wechseln die primitiven Neural- und Mesoderm-Segmente regelmässig mit einander ab. Die mesentodermale Segmentation ist dieselbe, die von v. Wijhe den Selachiern zugeschrieben wird."[1]

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[1] It is seen that Miss Platt finds the segmentation, both neuromeric and mesomeric, different in Squalus and Necturus. While in embryos of the former she

b. RELATION OF ENCEPHALOMERES TO SOMITES.

With Hoffmann ('94 and '96) I am able to confirm the presence of van Wijhe's head somites in Squalus (Acanthias) and also Platt's "anterior" somite. Valuable as this repeated confirmation appears to me, I regard as equally important the fact that anterior to the sixth (van Wijhe's) somite *a mesodermal segment corresponds to each of the primary encephalic vesicles* (encephalomeres I to VII). A topographic alternation, however, such as that affirmed by Miss Platt for the hindbrain region of Squalus and Necturus, I do not find. In the early stages of development van Wijhe's sixth somite lies opposite the posterior constriction of encephalomere VII, but this relation is soon lost. However, the numerical correspondence seems important, and I believe that it will be shown by a study of nerve relations that the correspondence is not without morphological significance.

c. SOMATIC VALUE OF THE PRE-OTIC MESODERM SEGMENTS.

Although it has been stated that the purpose of this paper is to discuss the nature of the neuromeric segmentation and the relations of neuromeres to other segmental structures, it seems to me not inconsistent with this purpose to inquire into the credentials of those mesodermal segments in the Selachian head which van Wijhe in his famous paper considered of somatic value. The confirmation of their presence in Squalus given by Hoffmann ('94 and '96) and myself ('96), while strengthening the belief in their permanency, which has been greatly shaken by the discovery of more numerous segments in other Selachii (Torpedo), by no means demonstrates their somatic value.[2] The dis-

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finds in the hindbrain region two more somites than were seen by van Wijhe ('82) and a numerical correspondence of these with the neuromeres, in the latter, on the contrary, she finds neuromeres corresponding with a somatic segmentation which is the same as that found by van Wijhe. She finds, therefore, it may be inferred, two less hindbrain neuromeres in Necturus than in Squalus. In embryos of Amblystoma I find, in agreement with McClure ('90), no neuromere corresponding with encephalomere IV of Squalus, i. e. there is one less neuromere in the Urodele than in the Selachian. Now, since I find a numerical correspondence of van Wijhe's somites with hindbrain neuromeres (encephalomeres III–VII) in the Selachian, it is clear that they could not likewise correspond in the Urodele. However, I have been unable to find evidence of pre-otic somites in Amblystoma, and therefore am unable to affirm or deny a correspondence of neuromeric and mesomeric segmentation in this form.

[2] It is a matter of great interest that the latest investigation upon Torpedo (Sewertzoff, '98) shows that the mesodermic segmentation in Torpedo and Pristiurus is the same. Thus van Wijhe's results receive repeated confirmation.

crepancy in the results of investigators of the mesomeric, as well as of the neuromeric, segmentation most certainly justifies Rabl's ('89) complaint of the hasty way in which investigators have given mesodermal segments somatic value. In no question of morphology to-day is conservative judgment more needed. Before stating my own evidence I will briefly summarize the arguments advanced by previous investigators for and against the somatic value of the mesodermal segments of the head.

(1) In addition to the evidence first stated by Marshall ('81), that the dorsal mesoderm of the head of Selachian embryos undergoes a segmentation independent of the segmentation of the visceral arches, van Wijhe ('82, p. 4) uses the following arguments for the somatic value of his somites: "(2) Dass die Länge der Somite sich im ganzen Körper gleich verhält. (3) Dass die obere Grenzlinie der Rumpfsomite ununterbrochen in diejenige der Kopfsomite übergeht. (4) Dass die untere Grenze der Somite sowohl im Kopfe als im Rumpfe nur wenig unter der oberen Grenze des Darmes liegt." The latter proof has been amplified by Killian ('91) from the evidence that the head somites are dorsal in relation to chorda, dorsal aorta, and epibranchial (medio-lateral) line. (5) Hoffmann ('94) and Miss Platt ('97) have confirmed van Wijhe's statement that the development of the somites begins in the neck region and proceeds continuously both posteriorly and anteriorly. Furthermore (6) the same constituent parts, viz. myotome and sclerotome, may be distinguished in the head as well as in the trunk somites (van Wijhe, '82, Killian, '91). To this Miss Platt ('91) adds (7) the evidence that, as in the case of the somatic musculature of the trunk, the muscles derived from the "anterior," the first, the second, and the third somites (rudimentary in the case of the anterior and somewhat modified in the case of the first somite) first appear in the median wall of these somites. Finally (8) there is a correspondence of the neuromeres and mesodermic segments throughout the entire length of the neural tube (Neal, '96).

The following are the arguments advanced in opposition to the somatic value of the mesodermal segments of the head.

(1) The divisions of the mesoderm of the head are due to the mechanical influence of the neighboring parts, chiefly that of the visceral pouches (Kastschenko, '88).

(2) The divisions are irregular in size (Kastschenko, '88, Rabl, '89).

(3) In van Wijhe's third proof there is "nicht die Spur eines Beweises für die Richtigkeit seiner Ansicht" (Rabl, '89, p. 234).

(4) The 1st somite is an exception to van Wijhe's fourth argument (Rabl, '89); moreover, the constrictions are never complete in the case

of the somites 2 to 5 (Katschenko, '88, Rabl, '89), so that it is impossible to state the position of their lower boundary with reference to the dorsal wall of the alimentary canal (Rabl, '89).

(5) The development of the "head cavities" is discontinuous with that of the trunk somites (Rabl, '89, Kupffer, '93). While the development of the pre-otic segments takes place later than that of the trunk somites, the differentiation of mesenchyma takes place much earlier in the head than in the trunk. This conflicts with the law, that in the Anlagen of serially homologous organs the older the Anlage the earlier the histological differentiation (Rabl, '89).

(6) There never appears in the case of the pre-otic segments a differentiation into myotome and sclerotome (Rabl, '89, p. 235).

(7) While the musculature of the trunk and occipital somites arises exclusively from the median wall of the somite, the musculature of the pre-otic segments has its origin in greater part from the lateral, and in smaller part from the posterior wall of the so called somites.[1] Moreover, while only a distinct and sharply defined portion of the trunk somites proliferates mesenchyma, the entire median wall of the pre-otic segments participates in the formation of mesenchyma (Rabl, '89).

(8) The topographic relations of the dorsal nerves in later stages are different in head and trunk. In the head the nerves grow laterad to the somites, while in the trunk they grow mediad to them (Rabl, '89).

Special arguments, in addition to the general ones stated above, concerning the nature of the anterior, the 1st, and the 2d mesoderm segments have been made, because of their marked peculiarities in development, structure, and relations, and of their important bearing upon the question of the morphology of the eye muscles. It will therefore be necessary to state these also.

Two chief opinions concerning the nature of the anterior (Platt's) and the 1st and 2d (van Wijhe's) mesoderm segments are now held: (1) that they are serially homologous with trunk somites (van Wijhe, Platt, Hoffmann, Neal, Fürbringer); (2) that they are abortive visceral pouches (Kupffer, '88, Froriep, '92, Sewertzoff, '95). The discussion, therefore, turns upon the question whether these structures represent diverticula (dorsal) of the mesoderm, or lateral diverticula from the alimentary canal.

Miss Platt ('91, '91^a) argues for the somatic value of the anterior somite (cavity) as follows: — (1) In position, independence, and time of origin this cavity resembles the following ones. (2) Many cells from its median wall migrate into the centre of the cavity, and cells bounding the inner wall above and below assume the elongated contour of muscle cells.

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[1] Balfour ('81) holds that both median and lateral walls of the trunk somites form the lateral trunk musculature.

Hoffmann ('94, p. 649) also, while not able to state with definiteness that the anterior cavity is a dorsal or lateral diverticulum from the alimentary canal, i. e. whether it represent a mesoderm segment or a visceral pouch, considers it probable that it represents the former, since it is very similar to the succeeding head cavities of van Wijhe. Hoffmann mentions the migration of cells into the cavity of the somite, but does not specify from which wall they are proliferated. He also states that from the walls of the somite "entstehen keine Muskelfasern" ('96, p. 256). Against these views of Miss Platt and Hoffmann no special arguments have as yet been raised.

The first somite of van Wijhe possesses the peculiarity of a median stalk connecting the somites of the opposite sides of the body.[1] The relations of this stalk to the dorsal wall of the alimentary canal, to chorda, and to dorsal aorta have been used as the chief criteria in contending for its dorsal or its ventral nature. The evidences that the first somite represents somatic (dorsal) mesoderm are as follows: (1) Its cells are proliferated from the dorsal wall of the alimentary canal (Platt, '91ª).[2]

[1] Such a median connection, however, also appears in the early stages of development of the "anterior cavities." The connecting stalk of the "anterior cavities," however, as stated by Hoffmann, never possesses a lumen, as does the median connecting stalk of the premandibular cavities.

[2] Miss Platt, in her earlier paper ('91, p. 81), states that the mesoderm of the premandibular cavity is formed, at least in part, by a proliferation of cells from the mandibular cavity, while in her later paper ('91ª, p. 256) she writes, "The most anterior mesoderm of the head does not take its origin from the mesodermic plates, but from the dorsal wall of the alimentary canal. The mesodermic plates end with the mandibular cavities." The lumen of the connecting stalk, according to Miss Platt, is, as stated by Marshall ('81), formed secondarily by the fusion of a median with the two lateral cavities. This evidence is interesting, since it bears on the question whether the cavity of the connecting stalk is to be regarded as a part of the archenteron, and would seem to answer this question in the negative. Killian ('91, p. 102), however, finds the connecting stalk a "Sklerotomkommissur," and thus, it is to be inferred, the lumen of the stalk, which according to his account is formed secondarily, not a part of the archenteron. He states (p. 102): "Erwähnt sei noch, dass zwischen den beiden ersten Mandibularsomiten vor dem vorderen Chordaende und über dem Aortensinus ein Mesodermzellenhaufen liegt, der die Sklerotomanteile beides Somiten in Verbindung setzt (Sklerotomkommissur). Was nun der Oralzone angeht, so entsteht sie dadurch, dass die vordersten Zipfel des ursprünglich schwalbenschwanzförmig endenden dorsalen Mesoderms die vordere Darmkuppe (vordere Ektodermtasche von Petromyzon nach Kupffer) über- und umwachsen, und so einen medianen Zellkomplex bilden, aus dessen hinterer

(2) Its connecting stalk is axial in position (van Wijhe, '82); dorsal to carotis (Dohrn, '88). (3) This section of the head cavity is so similar to the remaining sections, that it must be considered as serially homologous with them (Balfour, '81). Oppel ('90, p. 623), however, states (for Anguis) that "nur der histologische Bau und die Art der ersten Entstehung dieser vorübergehend im Mesoderm auftretenden Somiten gestattet, an der Deutung festzuhalten dass es sich hier in der That um Somiten handelt."

That the 1st cavity is ventral would seem to follow from the evidence that (1) it arises as an entodermic diverticulum from the prechordal portion of the alimentary canal (Seessel'sche Tasche), whose cavity is at first continuous with that of the alimentary canal (Kastschenko, '88, Kupffer, '88, '90, '93). "Streng genommen," says Froriep ('92^{a}, p. 589), "konnte es übrigens immer noch eher ventral, als dorsal genannt werden, wenigstens was sein Lumen und seine untere Wand anlangt. Denn das Aequivalent der Chorda, welche als Achsenfaden dorsale und ventrale Gebilde scheidet, ist selbstverständlich nur in der oberen Wand des medianen Verbindungsstückes zu suchen."[1] (2) The method of separation of the premandibular head cavity from the entoderm, as well as the presence of a median connecting stalk, serves to distinguish this from the following mesoderm segments (Kupffer, '93). (3) According to Kupffer ('94) the connecting stalk of the premandibular cavity is

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Hälfte für jede Seite ein Somit entsteht (van Wijhe's erster), während die vordere Hälfte zu Grunde geht." It is readily seen that this evidence tells decidedly against the view that the connecting stalk is ventral, and against the view of Kupffer and Froriep, that its lumen is a part of the archenteron.

Furthermore, Goette ('90) has given evidences concerning the method of formation of the anterior mesoderm in Ammocœtes which stands in direct contradiction with that stated by Kupffer, and, if true, takes away the chief support of the theory of the visceral-pouch nature of the anterior mesoderm in that animal. Goette writes: "Unbedingt muss ich aber die angeblichen 'Coelomdivertikel' des Urdarms im Kopf und Vorderumpf für täuschende Bilder erklären, was sich am Besten versteht, sobald man die Mesodermbildung durch die ganzen Schnittserien von vorn nach hinten verfolgt und dabei die vollkommene Uebereinstimmung derselben in allen Regionen antrifft. Ein Blick auf die Abbildungen lehrt, dass von einer verschiedenen Auffassung derselben nicht die Rede sein kann: giebt es im Rumpf keine Coelomdivertikel, so fehlen sie auch im Kopf. Auch die beiden 'präoralen Kopfhöhlen' sind weiter nichts als das erste Mesomerenpaar, welches allerdings wenn man seine erste Anlage in unmittelbarer Fortsetzung der folgenden Mesomeren übersah, später eine Ausstülpung des Urdarms vortäuschen kann, wie ich es weiter oben auseinandersetzte." Goette's figures, especially Figures 42, 43, and 44, strongly support his statements.

[1] Willey ('94, p. 175) accepts Kupffer's and Froriep's conclusions.

ventral to the dorsal aorta.[1] The vessel which Dohrn ('88) called the *carotis*, and which he stated lay ventral to the connecting stalk of the first cavity, if comparable at all, is comparable only to the *carotis ventralis* of Amniota.[2]

The chief arguments concerning the nature of the 2d (mandibular) cavity have already been given in connection with the general question of the pre-otic mesodermal segments, and it is therefore not necessary to repeat them here. The evidence of a continuous lumen between this cavity and the alimentary canal stated by Miss Platt ('91^a) has been interpreted by her as favoring the view that the cavity is formed as an outgrowth from the dorsal wall of the alimentary canal, similar to the mesodermal pouches in Amphioxus. Kupffer ('94), however, regards it as evidence in favor of his view, that these cavities are abortive visceral pouches. It is necessary, finally, to recapitulate a point in evidence which has only an indirect bearing on the question of the somatic value of the 1st, 2d, and 3d cavities, but which concerns vitally the morphology of the eye muscles (derived in Selachii from these cavities). It has been stated by Hatschek ('92) and Kupffer ('92–'96) for Ammocœtes (Petromyzon Planeri). Their results tend to show that the eye muscles of that low Vertebrate are, with the possible exception of the musc. rectus posterior (externus), derived from splanchnic and not from somatic mesoderm. According to Hatschek ('92), the musc. obliquus superior appears as a differentiated portion of the muscles of the velum, which correspond with the musc. adductores mandibulæ. His evidence (pp. 149, 150) is as follows: "Vom vorderen inneren Rande dieses Muskels [velar muscle] dringt nämlich ein Muskelfaserbündel dorsal in das Bindegewebe ein und zieht seitlich am Trabekel vorbei zwischen dem ersten und zweiten Trigeminusganglion hindurch bis in die Nähe des Auges, wo es im Bindegewebe zugespitzt endet. Von da beginnt — wie ein zweiter Muskelbauch — mit seinem zugespitzten hinteren Ende der musc. obliquus superior und zieht, wieder anschwellend, in gleicher Richtung weiter zum Auge. Die histologische Uebereinstimmung beider

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[1] Kupffer's statement applies to that cavity in Ammocœtes which has been homologized, in my opinion correctly, by most investigators (Balfour, Dohrn, Shipley '87, Kupffer) with the premandibular cavity of Selachii.

[2] In my opinion those writers who have quoted Balfour ('81) and Marshall ('81) as holding that the connecting stalk of the premandibular (1st) cavity is ventral have misunderstood them. They both spoke of the two lateral parts of this cavity as prolonged ventralwards to meet below the base of the forebrain. They give no proof that the stalk is morphologically ventral, and in my opinion speak of it as ventral only with reference to the wall of the brain.

Muskelteile ist eine vollkommene. Dieses Verhältnis ähnelt in hohem Grade jenem, welches van Wijhe als ein embryonales von den Selachiern abgebildet hat. Seine Deutung ist aber darin zu korrigieren, dass der m. obliqu. sup. nicht dem parachordalen Muskelblatte, sondern den Seitenplatten zugehört. Die übrigen Augenmuskeln, die in Form eines Kegelmantels an der medialen ventralen Seite des Augapfels sich finden, bilden in Bezug auf ihre Lage und histologische Beschaffenheit eine dritte Gruppe, deren Ableitung nicht ganz sicher erscheint. Sie sind wahrscheinlich von den Konstriktoren des Visceral-apparates abzuleiten. Keinesfalls können sie nach ihre Lage, Verlaufsrichtung und Struktur zu den Seitenrumpfmuskeln in Beziehung gebracht werden."

Kupffer's ('94) results are essentially a confirmation of those of Hatschek. Finding that the premandibular cavity entirely disappears, and that its cells contribute in no part to the formation of the eye muscles, Kupffer is led to doubt the conclusions of those investigators who derive the muscles innervated by the oculomotorius from the epithelium of this cavity. According to Kupffer all the eye muscles (with the possible exception of the musc. rectus posterior) are derived from two visceral arches, the "trabecular" and the mandibular. This evidence, as well as that given by Hatschek, obviously stands in direct contradiction to the somite theory. I am, however, after my study of the literature, inclined to be optimistic concerning the ultimate settlement of the question as to the somatic value of the pre-otic mesodermal segments, for the differences of opinion are not due to equivocal evidence, but to directly contradictory and equally positive statements. We have chiefly to determine who has stated the facts correctly in order to determine whether we shall accept the opinion of van Wijhe, or that of Kastschenko, Rabl, and Froriep. The evidence obtained by me, which leads me unhesitatingly to accept the view of the first, that the head somites are serially homologous with trunk somites, is as follows. I find the preotic mesodermal segments as described by van Wijhe ('82) most clearly defined by mesodermal constrictions or clefts in embryos of Squalus with 28 or 30 somites (Plate **3**, Fig. 13, Plate **6**, Fig. 40, Plate **7**, Fig. 46).[1] They are so distinctly marked that they may be seen in whole specimens properly cleared, as well as in sections. Moreover, they are found to be the same on both sides of the embryo.[2]

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[1] Van Wijhe's post-otic mesoderm segments have indisputable somatic value, and need not be brought into discussion.

[2] An examination of some finely preserved embryos of Torpedo ocellata, kindly given me by my friend, Professor A. N. Sewertzoff, leads me to agree with Sedg-

The contention that the constrictions between van Wijhe's somites are incomplete does not appear to me to militate greatly against the view that they have morphological value, inasmuch as their permanency has been repeatedly attested (van Wijhe, Hoffmann, Neal, and Sewertzoff). Nor does Rabl apparently consider this argument as of great weight, since he regards van Wijhe's 5th (1st post-otic) somite — though the constrictions which are found in front and behind are incomplete — as a true somite. The reduction in the myotomic portion of the dorsal mesoderm accounts in great part for the incompleteness of the constrictions. I believe that one who follows the development of the pre-otic and sub-otic mesoderm in Ammocœtes, and observes the ontogenetic dissolution of the compact dorsal mesoderm into loose mesenchyma, which follows the great enlargement of the nerve ganglia and of the otic capsule, is in a position to understand the reduction of the dorsal mesoderm in this region in Vertebrates higher in the phylogenetic scale than Ammocœtes.[1]

wick ('92), that this is not true of the mesoderm segments discovered by Dohrn ('90, '90^a) in that form. Dohrn apparently did not endeavor to ascertain whether they were symmetrical or not. I am unable to determine, even in carefully made reconstructions of well oriented frontal sections of embryos at the same stage of development as that described and figured by Dohrn ('90^a), whether or not there is a correspondence of the mesodermal segments on the two sides of the head anterior to the one which, in my opinion, corresponds with the 15th segment of Dohrn. While my own negative conclusions cannot be regarded as in any sense disproof of the segmental value of Dohrn's somites, it is my opinion that the evidence of their variability shown by the conflicting results of Killian ('91) tends to throw considerable doubt upon it. Since Killian ('91, p. 103) finds that of the anterior of these segments one is to be regarded as the sclerotome portion of a somite, while others are simply vesicular enlargements of the mesoderm of the mandibular arch, it is to be inferred that Dohrn subjected the head somites of Torpedo to little critical examination. To regard as evidence of somites all vacuolar spaces in the dorsal (and lateral!) mesoderm which appear between the somatopleure and splanchnopleure at the time these layers separate, seems to be too uncritical. Similar phenomena appear in the mesoderm of Squalus in those early stages of development, when the cœlom is in the process of formation, viz. in stages when the neural plate is widely expanded and the embryo possesses 4 or 5 somites. Recent studies by Sewertzoff ('98) render still more doubtful the results of Dohrn and Killian.

[1] A mechanical explanation of the constrictions between the head somites of van Wijhe, such as that offered, but without evidence, by Kastschenko ('88), seems hardly worthy of consideration. That such constrictions as those, for example, between somites 3 and 4, and 4 and 5, cannot result from the so called mechanical influence of visceral clefts, follows from the evidence already stated by Hoffmann ('94 and '96) that in Squalus, the constrictions lie dorsal to the visceral arches. I cannot, however, agree with Hoffmann that we may conclude from this evidence that the visceral arches are intersomitic in position, as are the ribs in the

The evidences of irregularity in size and discontinuity in development and differentiation are not, in my opinion, the more serious of the objections raised. Such differences may indeed be explained as cœnogenetic. Rabl himself has given the evidence ('89) that the first rudimentary visceral cleft is differentiated later than the second. Moreover, it is well known that the first rudimentary myotome in Amphioxus develops later than the following. Differences in time of development and of differentiation are to be expected when a comparison is made between the Anlagen of serial organs, some of which become highly differentiated (e. g. the eye muscle somites, 1st, 2d, and 3d), while the others (e. g. the anterior, the 4th, and the 5th somites) are becoming rudimentary. It is interesting to find that the last intersomitic constrictions to be formed are those between the anterior and the 1st cavity, and between somites 4 and 5, that is, the constrictions separating the most rudimentary somites. The separation of the anterior somite from the premandibular is first complete in an embryo with 26 or 27 somites, while the constriction between somites 4 and 5 appears first in an embryo with 28 somites. Consequently van Wijhe's statement, that the segmentation of the dorsal mesoderm begins in the neck region and proceeds continuously anteriorly and posteriorly, is true only in part. But it also follows that the discontinuity in the development of the more anterior constrictions may be explained as in great measure due to degeneration. The retardation in development due to degeneration, already apparent in the 1st somite of Amphioxus, makes itself manifest in the somites of the more highly specialized Squalus as far posteriorly as the 7th somite of van Wijhe (equivalent to the 8th somite of Amphioxus ?), which I believe to be *the first somite differentiated, as well as the first to develop a permanent myotome.*[1] The correlation between degeneration and retarded development serves to explain, for the occipital somites at least, why the development of the somites in the Craniota begins in the neck

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trunk. Such purely topographic relations in the Selachian cannot be regarded as weighty evidence in the settlement of this question, in comparison with the evidence stated for Amphioxus (van Wijhe, '93, Hatschek, '92), Bdellostoma (Price, '96^{a}), and Amphibia (Houssay, '91, Platt, '94), which has led these investigators to regard the visceral clefts as intersomitic in position. In view of the great probability of a shoving forward of the visceral clefts with reference to the somites in Squalus, I am unable to accept Hoffmann's conclusion on the basis of the evidence he presents.

[1] On account of the considerable variation in the length of embryos in early stages of development, I am unable to state positively that the seventh somite is the first to develop. It may be the eighth somite which does so, as stated by Hoffmann ('94, '96). The seventh somite shows some signs of degeneration, having a small myotome and losing its ventral nerve during development.

region. So far as I know, hitherto no explanation of this phenomenon has been suggested.

That which I have regarded as the more serious of the objections made by Rabl ('89 and '92), viz. that the pre-otic segments are not morphologically comparable with trunk somites, inasmuch as they do not show a differentiation into myotome and sclerotome, may be met by a denial of the statement, so far as it applies to the 3d somite of van Wijhe.[1] I have followed the development of this somite through closely connected stages of development, until it becomes converted into the musc. rectus posterior and assumes relation with the eye, in order to determine whether in its development it exhibits those marked differences which, as stated by Rabl, serve to distinguish pre-otic and post-otic mesodermal segments. The evidence which I have obtained may be summarized as follows: Cross sections of embryos in early stages of development leave no doubt that the 3d somite, as its topographical relations to chorda, dorsal aorta, epibranchial line, and dorsal wall of alimentary canal show, is composed of only dorsal mesoderm. Figure A represents a cross section in the region of this somite from an embryo with 28 somites (compare Plate **3**, Fig. 13). It is seen that a well marked cavity (myocœl), surrounded by a single layer of epithelial cells, may be distinguished.[2]

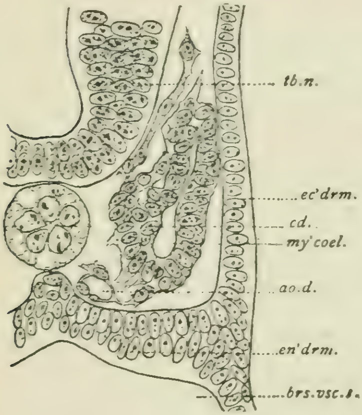

FIGURE A.

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[1] Both van Wijhe ('82) and Killian ('91) have affirmed a differentiation of head segments into myotome and sclerotome.

[2] That the epithelial walls of the cavity (Fig. A) are not continuous with the two layers of the lateral plates is due to the obliteration of these two layers caused by the great development of the first visceral pouch.

Fig. A. Cross section of a Squalus embryo in the region of van Wijhe's 3d somite and encephalomere IV. × 240. The dorsal nature of this mesodermal segment is attested by its relations to dorsal aorta and wall of alimentary tract. At this stage (Acranienstadium) the region of proliferation of mesenchyma is seen to be a definite one, and to correspond in its relations with the sclerotome of trunk somites.

ao. d., dorsal aorta; *brs. vsc. 1*, first visceral pouch; *cd.*, chorda dorsalis; *ec'drm.*, ectoderm; *en'drm.*, entoderm; *my'cœl.*, myocœl, enlarged ventrally to form a sclerotome vesicle; *tb. n.*, neural tube.

The cavity of the somite is enlarged ventrally opposite that portion of its median surface where a rapid proliferation and migration of cells appears to take place. I see no reason why the more dorsal and lateral portion of the mesoderm should not be homologized with the myotome portion, and the ventral median region with the sclerotome portion of trunk somites. I am unable to detect any essential difference between the phenomena presented in this section and those presented in sections made in the region of van Wijhe's 5th and 6th somites, to which Rabl grants "Bürgerrecht" as true somites. The greater dorsal extent of the latter cannot be regarded as an essential difference. Here, as there, we find a well marked and definite region of cell proliferation. As development goes on, the cavity of the 3d somite increases in volume, and at the same time the somite grows forward, chiefly by the elongation of its anterior end, median to the Gasserian ganglion. In confirmation of the statement of Miss Platt ('91), I find that the first muscle cells are differentiated in the median wall of that portion of the somite which at this stage lies posterior to the Gasserian ganglion. The great extension of the anterior portion seems to retard its histological differentiation. But in this portion also, when muscle cells appear, they are found in the median wall. Rabl ('89, p. 236) says: "Während ferner die Muskulatur der Urwirbel ausschliesslich aus der medialen Wand entsteht, nimmt sie im Vorderkopf zum grössten Theil aus der lateralen und zum kleineren Theil aus der hinteren Wand der sogenannten Somite den Ursprung." A cross section of the myotome of the 3d somite at a late stage of development appears to me to refute this statement (Figure B). It is clear from an examination of the phenomena presented in such a

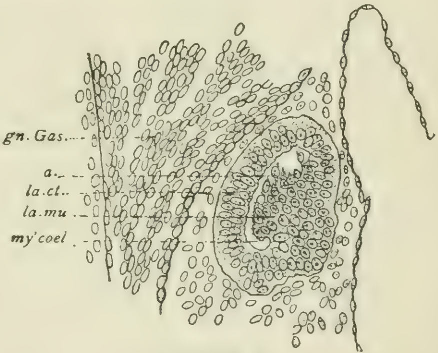

FIGURE B.

FIG. B. Portion of a cross section through the middle of the myotome of van Wijhe's 3d somite, in a late stage of development (20 mm.). Elongated muscle cells are already differentiated in the median wall (muscle plate), while the lateral wall (cutis plate) retains its epithelial character. × 50.

a, cell migrating from the median wall of the myotome into the myocœl; *gn. Gas.*, Gasserian ganglion; *la. ct.*, cutis plate; *la. mu.*, muscle plate; *my'cœl.*, myocœl.

section, that the greater part of the cells proliferated into the cavity of the myotome, the cells of which are at this stage already converted into elongated muscle cells, arise from its median wall. While the outer wall still maintains its primitive epithelial character, the inner wall has become many cells in thickness and some of these cells appear in the act of migrating into the now greatly diminished lumen of the cavity. Later, however, the cells of the outer wall also are converted into muscle cells, and thus both walls of the cavity participate in the formation of the musc. rectus posterior. We have therefore in the 3d somite of van Wijhe a pre-otic segment of the dorsal mesoderm, which becomes differentiated into myotome and sclerotome, and whose musculature is derived in greater part from its median wall. Furthermore, as is well known, its musculature is innervated by a nerve (abducens) which all the later morphologists, with, so far as I know, one exception (Kupffer, '94, '95), regard as a ventral nerve comparable with spinal ventral nerves. Finding this to be the case with at least one pre-otic mesoderm segment, we are in a better position than we otherwise should be to understand the more modified, or at least more divergent, conditions presented by the remaining pre-otic segments, viz. the anterior, the 1st, the 2d, and the 4th. That in these segments marked peculiarities appear is certain. In the 4th somite we have a segment of the dorsal mesoderm divided by constrictions from the 3d and 5th somites at a time when it presents essentially the same evidences of differentiation into myotome and sclerotome which appear in the 3d and 5th somites. That no muscle cells are formed in its inner wall, and that it soon breaks up into loose mesenchyma, are phenomena which are to be expected in a somite destined to become rudimentary. That it is more rudimentary than the 5th somite is due to the development of the otic capsule, under which it lies. The 5th somite — in whose inner wall elongated cells appear, without however developing into muscle fibres (as stated by Sedgwick, '92) — thus forms a natural transition to the conditions presented by the 4th. If the 3d and 5th are to rank as somites, it is in my opinion impossible to deny that the 4th, which lies between them, is serially homologous with them, even though it should lack some of the characteristics of a typical trunk somite.

Passing forward in the embryo to the 2d (mandibular) somite, it seems to me indisputable that this is the anterior continuation of the dorsal mesoderm. In very early stages it grows ventrally to form the mesoderm (mesothelium) of the mandibular arch, a process which, according to Kupffer ('88), occurs in Petromyzon also. However, only the dorsal part of the "mandibular cavity," which later becomes separated from the ventral to form the musc. obliquus superior, can by virtue of its topographic relations to chorda and aorta be regarded as the somatic portion of this mesoderm segment (Plate **7**, Fig. 56). Its ventral portion, which later becomes differentiated into the musc. adductor mandibulæ, is therefore splanchnic. While the indications of the differentiation of the 2d somite into myotome and sclerotome are less clearly expressed than in the case of the 3d and 4th, I have no reason to question the correctness of Killian's ('91) interpretation that such appear. The great enlargement of the cavity of the somite is the chief factor in modifying its form and the relations of its constituent parts. While Miss Platt ('91) finds the musculature to arise first in the median wall of the somite, that is to say, the *dorsal* part of the so called "mandibular cavity," Hoffmann ('96) states that the musc. obliquus superior arises in its upper and lateral walls. In my opinion their conclusions are not so divergent as they might at first sight seem to be, for I believe that the portion of the somite which Hoffmann calls dorsal is morphologically *median;* in other words, that it is the portion which in early stages lies against the wall of the neural tube (Plate **7**, Fig. 56). I agree with Hoffmann that the musc. obliquus superior arises in the dorsal and lateral walls of the second (van Wijhe's) somite, but with the qualification that the dorsal wall is morphologically median.[1]

The first (premandibular) somite shows in its development even greater peculiarities than those of the mandibular; yet it appears to me to possess somatic value as unquestionably as the latter does. The first and most important question to answer is whether this segment represents dorsal mesoderm or a diverticulum from the alimentary canal, and for this purpose the relations of the connecting stalk furnish us with the decisive evidence. In a median sagittal section of an embryo with 14 or 15 somites, such as that shown in Figure C, the tissue which is later differentiated as the connecting stalk of the first somite appears as a mass of cells between the base of the brain, in that region which lies just posterior to the pit of the infundibulum, and the dorsal wall of the alimentary canal. Posteriorly this mass of cells is continued into the chorda and its relations are seen to be such that, if the chorda is dorsal, so must the mass of cells be also. The lumen of the alimentary canal may be traced to a point directly ventral to the pit of the infundibulum, where it ends as the so called "Seessel'sche Tasche" (Kupffer's "präorale Darm"), while its walls become continuous anteriorly with that mass of tissue which later differentiates into the "anterior cavities." Furthermore, a cross section of a corresponding stage of development in a plane immediately posterior to the infundibulum (i. e. along the line α β of Figure C) gives equally convincing evidence (shown in Figure D) that the mass of cells (1) lies *dorsal* to the wall of the alimentary canal, with which, however, they are in close connection in this somewhat earlier stage (11–12 somites). There exists not the faintest shadow of evidence that the mass of cells which forms in its lateral part the premandibular cavities and in its median part their connecting stalk, represents entodermal diverticula. During development, as the result of the ventral growth of the infundibulum, the pre-oral (Seessel's) pouch becomes obliterated and the mass of cells surrounding the "anterior cavity" is cut off from those posterior to the infundibulum (26–27 somites). By this change in relations the Anlagen of the connecting stalk and of the premandibular cavity take a position apparently *anterior* to the alimentary canal and in close

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[1] Miss Platt's ('91^a) evidence of the continuity of the cavity of the alimentary canal and that of the mandibular cavity, as well as her evidence of two segments in the latter, appears to me illusory.

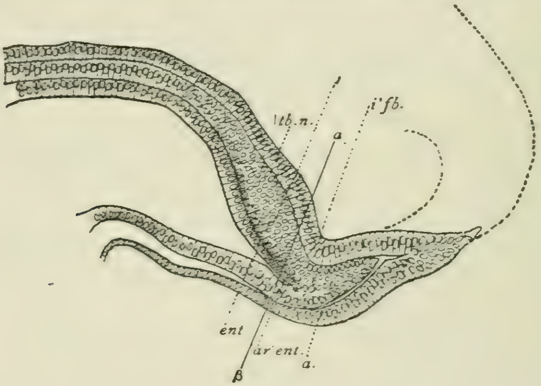

FIGURE C.

FIG. C. Median sagittal section of a Squalus embryo with 14 or 15 somites. The neural folds have not as yet met in the mid-dorsal line. × 77. The mesoderm of the connecting stalk of van Wijhe's first somite is seen as a thickened mass of cells lying between the base of the brain and the dorsal wall of the alimentary tract.

1, mesoderm which later becomes differentiated as the connecting stalk of the first head cavity. *a*, mesoderm of the "anterior cavity" (Platt); *ar'ent.*, pre-oral pouch of the archenteron; *ent.*, dorsal wall of alimentary canal; *i'fb.*, infundibulum; *tb. n.*, ventral wall of the neural tube; α β, projection of plane of the section shown in Figure D.

connection with the ectoderm immediately posterior to the infundibulum. Still later (40 somites) cavities appear both in the median connecting stalk and in the lateral mesoderm, and these by their fusion form the continuous cavity in the manner already described by Miss Platt ('91^{a}). It follows therefore that the premandibular cavities comprise dorsal and only dorsal mesoderm,[1]

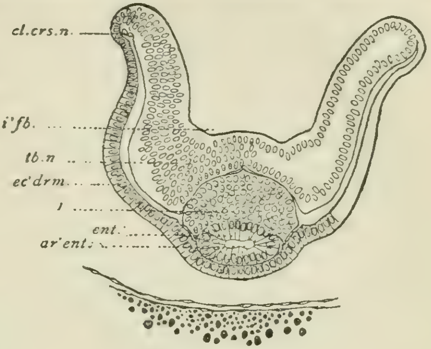

FIGURE D.

FIG. D. Cross section of a Squalus embryo with 11 or 12 somites in a plane corresponding with that of the line $\alpha\ \beta$ of Fig. C. × 50. The section shows clearly the dorsal position of the connecting stalk of van Wijhe's first somite (I) in relation to the pre-oral pouch (*ar'ent.*).

I, mesoderm of the connecting stalk of van Wijhe's first somite; *ar'ent.*, archenteron = pre-oral pouch; *cl. crs. n.*, neural-crest cells; *ec'drm.*, ectoderm; *ent.*, entoderm; *i'fb.*, infundibulum; *tb. n.*, neural tube.

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[1] Hoffmann ('94, p. 648), however, finds evidence of a splanchnic portion of the premandibular somite in a "Zellstrang, welcher dem Mandibularbogen parallel verläuft und der Vorderfläche deises Bogens unmittelbar aufliegt" (his Fig. 4 x, p. 648). He adds, "Ein Lumen dieses Bogens habe ich im diesem Strange nie gesehen," and he uses this evidence to support his conclusion that the mandibular arch is double. I can confirm Hoffmann's statement as to the presence of this "Zellstrang" in the anterior portion of the mandibular arch; but there is another cord, not mentioned by Hoffmann, which is in every respect similar to this one and extends parallel and close to the *posterior* wall of the arch. I hold Hoffmann's interpretation, however, to be incorrect, since, according to my determination, the cells of these strands are in large part if not entirely ectodermal in origin, i. e. derivatives of the neural crest. The cells of the Anlage of the Trigeminus may be followed in closely connected stages as they migrate ventrad until they enter the mandibular arch, where they come to surround the mesothelium as a ring of loose cells between the mesothelium and the superficial ectoderm. This evidence confirms the previous results of Kastschenko, Platt, and Goronowitsch ('93). While the fate of these cells is not clear to me, Miss Platt ('94 and '97) finds that in Necturus they contribute in large part to the formation of the cartilage of the mandibular arch. Considering the similarity in the origin of the anterior and posterior cell strands, as seen in parasagittal sections through the mandibular arch, it becomes noteworthy that Hoffmann ('94) in his preliminary paper failed entirely to reproduce in his figures the posterior, while in his later paper ('96, Taf. III. Fig. 22), he figures two cell strands as histologically quite different from each other. This appears to me a notable illustration of the prejudicial influence of a theory. Although I

and it may also be inferred that the median portion of the connecting stalk is morphologically the undifferentiated anterior portion of the chorda, while the more lateral portions of the connecting stalk may be regarded, as they have been by Killian ('91, p. 102), as representing the sclerotome of the somite. Furthermore, the inference drawn by Froriep ('92^a), on the ground of evidence presented by Kastschenko ('88) and Kupffer ('88, '90, '94), that the lumen of the connecting stalk must be ventral and morphologically a part of the procœlom, receives no support. If Kupffer's statement that the premandibular cavities of Ammocœtes are formed as diverticula from the alimentary canal is correct, their development in Ammocœtes must differ essentially from that in Squalus. Goette ('90), however, flatly contradicts Kupffer's statements. My own observations on Ammocœtes lead me unhesitatingly to accept the evidence presented by Goette.[1] Besides, the criteria furnished by the study of the early stages of development of the premandibular cavity in Squalus seem to me more satisfactory, because more decisive, than the evidence used by Kupffer ('93^a, p. 522) to demonstrate the ventral nature of the connecting stalk of the premandibular cavities in Ammocœtes, viz. the relation to a blood-vessel which is only hypothetically the complete homologue of the dorsal aorta. I find this blood-vessel in embryos of Ammocœtes of somewhat advanced stages of development (4 mm.) extending above the connecting stalk of the premandibular cavities, as the apparent anterior continuation of the dorsal aorta, as stated by Kupffer. But there is also ventral to the connecting stalk a similar blood-vessel, which unites with the dorsal vessel both anterior and posterior to the connecting stalk. It is consequently difficult for me to comprehend why the more dorsal vessel rather than the more ventral one is to be regarded as the anterior continuation of the dorsal aorta. Kupffer gives no reasons, simply stating that the ventral vessel can be homologized, if at all, with the carotis ventralis of Mammalia. Now, if we are to apply rigidly such a criterion as Kupffer's to

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am unable to accept Hoffmann's conclusion on the basis of the evidence he presents, I believe there are good grounds for holding that a visceral arch, which once existed between the mandibular and the hyoid (first and second visceral) arches, has disappeared in phylogeny. The evidence in favor of this view will be summarized later.

[1] That Kupffer has not in his studies come to a right understanding of the development of the anterior head mesoderm seems to me certain from a comparison of my sections with those figured by him ('90, Figg. 31 und 32, Taf. 28). The cells which he calls ganglionic are in my opinion the anterior mesoderm. This appears to me to be Kupffer's fundamental error.

determine what is dorsal and what is ventral, it would follow from the evidence already stated by Platt ('91) that the anterior portion of the dorsal aorta in Squalus embryos comes to lie in part *dorsal* to the chorda, and therefore that this organ, commonly known as chorda *dorsalis*, could more correctly be named chorda *ventralis*. Kupffer's argument thus leads to a *reductio ad absurdum*.

According to Hoffmann ('96) the muscles innervated by the oculomotorius have their origin from the posterior part ("Fortsatz") of the premandibular cavity. Because of the complicated development and the secondary subdivisions of this cavity, it is difficult to be certain; yet it seems to me that, as in the case of the second and third cavities, the epithelium of both median and lateral walls participates in the production of the muscles formed from this cavity, viz. musc. obliquus inferior, and recti inferior, superior, and anterior.

Before passing to a consideration of the nature of the "anterior cavities," I wish to discuss, in connection with the preceding study of the morphology of the eye-muscle somites in Squalus, the evidence of the development of the eye muscles of Petromyzon which has been given by Hatschek ('92) and Kupffer ('94), and to determine in how far this brings us to an understanding of the morphology of the eye muscles in Vertebrates in general. The repeated confirmation of Marshall's conclusion that the eye muscles in Selachii and Reptilia are derived from the epithelium of the first, second, and third cavities — van Wijhe ('82), Dohrn ('85), Orr ('87), Kastschenko ('88), Miss Platt ('91), Oppel ('92), Hoffmann ('96), and myself — seems sufficient to remove any doubt (so far as those groups of animals are concerned) which Kupffer ('94) may have sought to throw upon that conclusion. In Amphibia, Birds, and Mammals, as is well known, the eye muscles are differentiated from the connective-tissue capsule surrounding the eye. Although the source of these cells is not known with certainty, there is no reason to doubt that, as in Selachii and Reptilia, they have their origin from the dorsal mesoderm. In direct contradiction to these facts, which hold true for higher Vertebrates, stand the conclusions of Hatschek and Kupffer, that in Cyclostomes the eye muscles are splanchnic in their origin, i. e. derived from the mesoderm of the visceral arches. Let us examine the evidence given by them, in order to determine in how far it seems to warrant their conclusions. Hatschek's briefly summarized evidence has been stated on pages 192, 193, and needs no repetition.

In sections of a 5 cm. Ammocœtes I find the relationship of the median posterior musculature of the eye capsule to the velar muscle, which is the probable homologue of the musc. adductor mandibulæ of Selachii, to be those stated by Hatschek. Whether in this muscle group we have to do with the musc. obliquus superior, I am not able to state, since its innervation still remains uncertain to me.[1] I know, however, that it is not innervated by the oculomotorius. Its fibres, moreover, are not continuous with those of the velar muscle at this stage of development, if indeed they are at any stage. Hatschek's chief evidence that this muscle is derived from the velar muscle apparently consists in their histological resemblance, which he states is complete. At the stage studied by me this is certainly untrue. For I find that while the velar muscle is composed of large fibres, at least 7μ in diameter, the fibres of the muscle in question are in their widest part not over 3μ in diameter, and also that, while the fibres of the former show well marked longitudinal and cross striations, those of the latter show these very faintly. Moreover, the nuclei of the former are for the most part round or oval, while those of the latter are exceedingly elongated. It is of course possible that Hatschek bases his statements on the examination of the histological conditions in embryos of a different stage of development. But even if we grant that the musc. obliquus superior in Cyclostomes is, as in the Selachii, derived from the dorsal part of the musculature of the mandibular arch, this evidence no more warrants the conclusion that the muscle is splanchnic in origin in the former group than in the latter. Of its dorsal origin and somatic nature in the latter group, proof has been given above.

Even more theoretical than his conclusions concerning the origin of the musc. obliquus superior appears Hatschek's inference that the eye muscles innervated by the oculomotorius are derived from the constrictors of the visceral arches, a conclusion which he draws apparently by the method of exclusion. It does not seem to have occurred to him that these muscles may have had their origin from the connective-tissue capsule of the eye, the cells of which are in my opinion derived from the dorsal mesoderm in this region, which in early stages becomes disintegrated and surrounds the eye vesicle. Kupffer ('94) thinks that the more difficult part of the task of tracing the development of the eye musculature in Ammocœtes is accomplished when he has followed the growth of muscle cells from the so called "Trabekular" and the mandibular arches until they come into close relation with the eye capsule in a 6 mm. embryo. In consideration of the facts that he does not even know that these muscle cells become differentiated into the eye muscles, and that he has not determined their innervation, the doubt which he seeks to throw upon the results which differ from his own appears quite unwarranted. Furthermore, I find that the anterior and posterior velar muscle strands described by Kupffer are in essentially the same relations to the eye capsule in stages of 6–9 mm. as in those of 5 cm., and that these strands show no relation — except that relation of the posterior (mandibular) muscle strand described by Hatschek ('92) — to the eye muscles, which are already clearly differentiated in the latter stage. I must therefore conclude that Kupffer has not seen the early stages of the development of the eye muscles of Ammocœtes. I regard the determination of their origin in this animal as an embryological task yet to be accomplished, — a task in which the well known difficulty of obtaining material in stages between 9 mm. and 30 mm. will be encountered. For it is in these stages, in my opinion, that the eye muscles are differentiated.

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[1] That Hatschek ('92) incorrectly identified the musc. rectus posterior, has been shown by M. Fürbringer ('97) from the study of its innervation, a matter to which Hatschek seems to have paid no attention.

I turn now to the development of the "anterior cavity," which has been so thoroughly studied by Miss Platt ('91, '91^{a}) and by Hoffmann ('96) that I need say but little, and that of a general nature. It seems very clear, since the "anterior" mesoderm segment develops from a perfectly solid mass of cells anterior and lateral to the infundibulum of the brain, that the statement of their formation as lateral diverticula of the alimentary canal is purely hypothetical. It seems also warrantable to infer that the connecting stalk which unites the lateral halves of the segments in early stages of development, the cells of which according to Hoffmann ('96) entirely disappear, represents in part the anterior continuation of the alimentary canal. But it is impossible to state, because of want of such criteria as chorda and dorsal aorta, whether we have here to do with dorsal mesoderm. Without proof to the contrary, and with the evidence that these cavities assume a histological appearance similar to that of the following ones, I conclude with Platt and Hoffmann that the "anterior" mesoderm segment, which appears, so far as is known, in only two Selachii (Squalus and Galeus), is serially homologous with those behind it. I am able to confirm the evidence given by these two observers, that mesenchyma cells migrate into the lumen of the cavity in the later stages of its development, and to confirm the former, that such cells first migrate from the median wall (Figure E), in which also some cells assume an elongated spindle form, possibly indicating rudimentary muscle cells. Such histological evidence would seem to tell in favor of the view that this mesoderm segment, like the following ones, is to be regarded as of somatic value.[1]

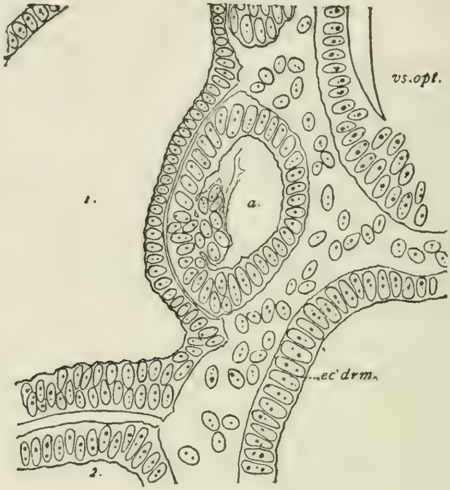

FIGURE E.

d. SUMMARY.

Neuromeres and somites show an exact numerical correspondence throughout the length of the embryo. The serial alternation of myelomeres and somites evinces the metamerism of the former, while the exact numerical correspondence of the encephalomeres and head somites appears equally convincing evidence of the metameric value of the encephalomeres. The head somites in Squalus are homologous with those described by van Wijhe ('82) for Scyllium and Pristiurus, and there is yet another anterior to these, viz. the "anterior" somite first

[1] As the most anterior of the cavities of the Selachian embryo, it would seem more probable that the anterior cavities described by Miss Platt should be homologized with the "head cavities" (vordere Entodermtasche) of Amphioxus, than that the next following, the premandibular, should be.

FIG. E. A cross section through the "anterior cavity" (frontal section of the embryo) in an embryo with 78 somites. × 240. To show the proliferation of cells into the myocœl from the median wall of the cavity.

1, 2, first and second head cavities; *a*, "anterior cavity" (Platt); *ec'drm.*, ectoderm; *vs. opt.*, optic vesicle.

seen by van Wijhe in Galeus. The somatic value of the post-otic head somites is indisputable. The pre-otic somites, five in all, are also in my opinion homodynamous with trunk somites. They are segments of the dorsal mesoderm (with the possible exception of the "anterior"), which, as exemplified in the third somite (van Wijhe's), become differentiated into myotome and sclerotome. While the "anterior" and the fourth somites become rudimentary and develop no muscle fibres, the eye muscles are differentiated from the median and lateral walls of the first, second, and third. The eye muscles of Selachii are therefore somatic in their origin, not splanchnic,[1] as has been held by Hatschek ('92) and Kupffer ('94). It will furthermore be shown that the nerves which supply them are serially homologous with ventral spinal nerves. It is to the consideration of the nerve relations that I now pass.

VI. The Relation of Neuromeres to Nerves.

Ahlborn ('84^a) said: "Es bleibt auch im Auge zu behalten, dass die gesammte Neuromerie secundärer Natur ist: sie ist nur eine Wiederhohlung aller vor ihr entstandenen Metamerien des Körpers. Eine primäre Metamerie, wie sie z. B. im dorsalen Mesoderm vorliegt, ist weder im centralen, noch im periferischen Nerven-system vorhanden,[2] und wenn im Rumpfe die Neuromerie mit der primären Mesomerie übereinstimmt, so reicht diese Eigenschaft im Allgemeinen nur so weit, als die Nerven sich innerhalb des primär segmentirten Mesoderms befinden, und sie hört auf, wenn die Nerven in solche Organe eintreten, die ausserhalb der Mesomeren liegen, oder die in einer anderen nicht segmentalen Metamerie entwickelt sind."

In the trunk, the arrangement both of myelomeres and nerves is clearly metameric, being correlated with the segmentation of the mesoderm. Related to each mesodermal somite is a ventral nerve (motor root), which arises from segmentally arranged groups of ganglionic cells in the anterior (ventral) horn of the spinal cord, that is, from each myelomere. Into the posterior (dorsal) horn pass the fibres of the dorsal nerve, which have their peripheral distribution in the skin of that segment (rami cutanei) and in the intestine (sensor and motor sympathetic fibres).

In a study of the simple, and it has been assumed primitive relations in the trunk, it is important to consider not only the peripheral distribution of nerve fibres, but also their distribution in the central nervous system. Gaskell ('89) has rightly insisted that the position of the cell groups which are in connection with the nerve fibres, is the true criterion of what forms a nervous metamere, rather than the position of the exits of the nerve fibres. The shifting of nerve roots is too well known to need discussion here. In regard to sensor nerves Miss Platt ('96) says: "Both development and comparative anatomy tend to show that it is a matter of little moment whether these fibres [of the lateral-line nerves] enter the brain by one nerve root or another." I find as a result of my own studies that the ganglionic cells of cranial nerves enter into fibrillar relation with the neural tube at points quite widely separated from the encephalomere from which the cells were proliferated, and also that in embryos of different Vertebrates the relations of the fibres of the same nerves to the encephalomeres are variable, not only in the case of ganglionic roots but of medullary roots also, as those of the trigeminus, abducens, and glossopharyngeus. In the swine and the chick the abducens arises from encephalomere VI, whereas in S. acanthias it is in relation with encephalomere VII. Also in swine and chick the root of the glossopharyngeus is in relation with encephalomere VII, whereas in S. acanthias it passes from the neural tube posterior to this neuromere. It is obvious, then, that we must take into consideration, particularly in the case of cranial nerves, both the location of the "Kerne" of the medullary roots, and the points or regions of proliferation of the ganglionic cells of ganglionic roots, in order to determine their primitive relationships.

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[1] With the exception of the musc. rectus posterior (Hatschek).

[2] Compare Froriep ('94).

a. Historical Review.

An examination of the literature bearing on the question of the relation of nerves to neuromeres is rendered difficult by the fact that many investigators have failed to distinguish between medullary and ganglionic nerve relations, and thus have not made clear what they meant by the statement that a nerve "develops" from, or has its "origin" from, the expansion or constriction of a neuromere. The figures of McClure ('90) and of Waters ('92), for example, show a proliferation of the ganglionic Anlagen of nerves from the neuromeres, but not the relationship of the neuromeres to *nerve fibres.* While it seems very probable that the proliferation of ganglionic Anlagen has a bearing on the primitive relationship of the dorsal nerves (sensor portion), our best criteria of the segmental value of encephalomeres, as well as of myelomeres, is their relation to medullary nerves, — i. e. ventral nerves and the motor components of the dorsal nerves. Furthermore, we must determine the primitive relations of medullary nerves, not by the place of exit of their fibres (i. e. by their roots), for we know these to be variable, but by the position of their "Kerne" in the walls of the neural tube.[1]

There is considerable difference of opinion as to whether nerves ("roots") arise primarily from the expanded portion of the encephalomere (or myelomere), or from the constrictions between these segments. As early as 1878 Marshall said, "My investigations tend very strongly to prove that all the nerves arise primitively from the widest parts of the dilated vesicles, whether of brain or cord, and never from the intervening constrictions." Later, McClure ('89), who is in agreement with Marshall as well as with Orr, Béraneck, and Waters, said, "The dorsal roots of spinal nerves take their origin from the apex of their respective myelomeres in exactly the same manner as the nerves of the medulla do from their respective encephalomeres." Minot ('92) criticises McClure for overlooking the fact that the "neuromeres can have no genetic relation to the ganglionic nerves." The ground of Minot's statement does not seem to me to be so self-evident as not to be in need of explanation.[2]

In disagreement with McClure, Miss Platt ('89) claimed that "the concavity in both medulla and spinal cord is the source from which the nerve originates," and her conclusion, which Minot accepts, is that the origin from the expanded portion of the neuromere is secondary. In view of this difference of opinion it is of interest that Balfour ('85) stated that in Selachian embryos the dorsal and ventral roots of spinal nerves alternate with each other, the dorsal roots being intersegmental (intersomitic) and the ventral roots segmental (somitic) in position. Miss Platt did not, however, in her statement of nerve relations make a distinction between dorsal and ventral nerves.

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[1] The most serious obstacle to the use of this criterion is the difficulty of applying it in those early stages of development when metameric relationships appear least modified. Martin ('90 and '91, p. 230) has noted an ontogenetic ventral shifting of motor "Kerne" in the cat.

[2] It is to be regretted that McClure gave no figures of the nerve relations of myelomeres. Minot apparently assumes that the neuromeres are constituted solely in adaptation to a motor segmentation, and therefore that the neuromeres are segmental localizations of ganglionic cells (i. e. motor "Kerne") in the wall of the neural tube, just as are the segmental ganglia of Annelida. It seems to me therefore that McClure might have met Minot's criticism by reminding him that neurologists have recognized in the medulla groupings of ganglion cells which are in relation with sensory fibres, i. e. sensory "Kerne" or "Endkerne" (see Edinger, '96, p. 366), and may well contribute to the metameric enlargements.

b. Nerve Relations in the Trunk of S. acanthias.

An examination of sections in the trunk region of embryos of S. acanthias leaves no doubt whatever that the chief proliferation of ganglionic cells occurs in the regions of constriction between myelomeres, i. e. opposite the somites, and that the ventral roots also arise opposite the somites. Motor roots appear long before the sensor roots, as was first stated by Sagemehl ('82). Dohrn has affirmed that they arise as early as Balfour's stage H. I find them in embryos of S. acanthias in which 34 somites are differentiated, stage H. From the very first, i. e. at this early stage, they are in relation with the ventral portion of the neural tube at a point directly opposite the middle of the somite. That the relation with the tube is opposite the *middle of the somite* is most easily demonstrated in frontal sections (see Plate **6**, Fig. 42, which represents a frontal section of an embryo with 50 somites); but that their relation is with the *ventral* wall of the tube, is most clearly seen in cross sections (Plate **6**, Fig. 41, *rx. v.*). In frontal sections more dorsally situated than those which show the ventral roots, the spinal ganglia are likewise seen to lie opposite the middle of the somites[1] (Plate **6**, Fig. 43). In later stages, however, the spinal ganglia lie opposite the anterior portion of the somites, i. e. intersomitic in position, as a result, probably, of the shifting of the somites. Since by this time the constrictions between myelomeres have disappeared, *it is quite impossible to state that dorsal roots arise either from the constrictions or from the dilatations of the myelomeres.*

McClure ('90, p. 42) has said that in the forms studied by him "the dorsal branches of the spinal nerves pass from the external surface of the myelomeres to the space between two somites, which is opposite their point of origin, and fuse with the epiblastic thickenings to form the spinal ganglia." Such a statement, if true, is certainly of great importance in settling the question of the morphology of cranial nerves. For it is now generally stated by morphologists that the chief distinction between spinal and cranial nerves consists in the fact that the ganglia of cranial nerves receive cellular material during development from the ectoderm of the lateral surface of the head, whereas the spinal ganglia do not. So far as I know, McClure's statement remains unconfirmed, and it is certainly not true for Squalus, and not true, so far as I am able to determine, for Amblystoma. In Petromyzon, however, as has been previously stated by Scott ('87) and Shipley ('87), the spinal ganglia lie opposite the constrictions between the somites (in later stages opposite the myosepta).[1] Thus, inasmuch as the dorsal nerves of Ammocœtes are *intersomitic* and never unite with the ventral nerves which are *somitic* in position, and inasmuch as the dorsal ganglia show close connection with the ectoderm in early stages of development and lose this connection during development, the spinal nerves of this animal form a natural transition from the nerves of Amphioxus to those of Squalus and higher Vertebrates. For in Amphioxus ventral nerves are somitic in position, dorsal nerves intersomitic, and the connection of the ganglia of the latter with the skin is retained throughout life.[2] Two chief causes seem to have brought about the change in the relations of the dorsal spinal nerves in the Vertebrate series. The first cause appears to have been the great dorsal and anterior extension of the trunk myotomes, and the second cause the posterior extension of the ramus cutaneus dorsalis vagi (ramus lateralis vagi), which takes the place of the rami cutanei of the spinal nerves. The physiological reason for the extension of the vagus is to be found in the advantage obtained from the centralization of sensory impulses in the brain. With van Wijhe ('92), Hatschek ('93), and M. Fürbringer ('97), I accept the theory of Prochaska, Sömmering, and Gegenbaur that cranial and spinal nerves are homodynamic, and the view of Hatschek ('92) that dorsal and ventral nerves primitively alternated with each other.[3] Of these, the former were mixed in function and the latter motor, as in Amphioxus.

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[1] Similar relations of dorsal ganglia and ventral roots have been shown by Marshall ('78, Plate III. Figs. 27 and 28) for birds; by Hoffmann ('90, Taf. CLV. Fig. 7) for reptiles; by Dohrn ('91, Taf. V. Figg. 16 und 17) for Selachii; and by Sewertzoff ('95, Taf. V. Fig. 16) for Amphibia.

c. NERVE RELATIONS IN THE CEPHALIC REGION OF S. ACANTHIAS.

In the head, where the nerve relations are much more complicated, it will be necessary to trace the development of the nerves in different stages. The series represented in Figures 7 to 21 (Plates **3** and **4**) is intended to show the changes which the neural crest (colored in blue) undergoes, and likewise to show the development of the brain vesicles up to the time when a fibrillar connection of the nerves with the neural tube is effected and the chief peripheral branches are differentiated.[1]

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[1] Because of this relation to the myomeric constrictions in Ammocœtes and the relation of the ganglia to the *expansions* of the spinal cord (myelomeres) deducible from it, it is obvious that not very great morphological value can be given to the fact that in Squalus the ganglia lie opposite the *constrictions* of the spinal cords.

[2] I hold with Hatschek ('92) and M. Fürbringer ('97) that in Amphioxus the homologues of the dorsal ganglia of Craniota are found in the cell groups at the place where the dorsal nerves meet the skin.

[3] See also Ransom and Thompson ('86).

Minot ('92) and Mitrophanow ('93) have stated that the neural crest in Selachii is not differentiated before the closure of the neural tube, and Rabl ('89) found that in Pristiurus embryos the "Trigeminus Anlage" first appears at a stage with 18 somites. On the other hand, Beard ('88) and Dohrn ('90) have shown that in some Selachii,[2] as well as in Sauropsida, the neural crest is differentiated in the region of the head before the closure of the neural tube.

As has been previously stated, my observations confirm those of Beard and Dohrn, since I find that at an early stage, when the cephalic plate is still widely open, the fundament of the trigeminus is clearly differentiated from that portion of the neural plate which is destined to form the neural tube. The disassociation of the neural-crest cells in this region and their resultant loss of compact arrangement have taken place to a considerable extent before the neural folds meet in the mid-dorsal line. Usually the neural folds first close in the trunk region behind the cephalic plate, and later in the region of the midbrain, i. e. in the region of the "Trigeminus Anlage." The closure of the cephalic plate occurs last in the forebrain, where the "neuropore" persists for a considerable period.

At a stage with 15 or 16 somites (Plate **3**, Fig. 7), when the cephalic plate is closed except in the region of the forebrain, the neural crest is clearly differentiated in that region of the brain which extends from the constriction between forebrain and midbrain to the anterior constriction of hindbrain neuromere (encephalomere) IV, i. e. in the region of the so called cephalic flexure. In the region of encephalomere IV a few cells with protoplasmic processes occur in the space between the neural tube and the overlying ectoderm. These may indicate that at one time this encephalomere was a region of cell proliferation and thus possessed a neural crest; but since the cells soon disappear, and since no new ones take their place, this encephalomere may be said to be a region of the neural tube which now (in S. acanthias) possesses no neural crest. That portion of the neural crest which arises anterior to this neuromere has been variously called "Trigeminus Anlage," "germe du

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[1] A study of the histogenesis of nerve has been made only in the case of the eye-muscle nerves, whose morphology still remains a matter of much dispute.

[2] I am surprised by Hoffmann's ('94) statement that in S. acanthias the trigeminus Anlage first appears in an embryo with 17 somites, that is, after the closure of the neural tube.

Trijumeau" (Mitrophanow, '93), and "erste periaxiale Strang" (Goronowitsch, '93). Its cells at this stage (15 or 16 somites) have already migrated half way down the side of the neural tube (Fig. 7). In the region of encephalomere V the disassociation of the cells of the neural crest has begun, and the dorsal part of the encephalomere in consequence appears enlarged. A ventral migration of its cells, however, does not take place until a later stage.

In an embryo of 18 or 19 somites (Plate **3**, Fig. 8) two regions of cell proliferation, separated sharply by encephalomere IV, are seen. Mitrophanow ('93) has stated that at the beginning the facialis is not wholly separated from either the trigeminus or the vagus group. I find on the contrary, as already stated, that no neural crest is found in the region of encephalomere IV, and that consequently the "Trigeminus Anlage" is separated by the space of this encephalomere from the posterior portion of the neural crest. Apparently as a consequence of cell proliferation and migration, the dorsal wall of encephalomere III is very thin at this stage, while that of encephalomere IV is considerably thicker and its cells are more compactly arranged. The cells of the neural ridge which form the "Trigeminus Anlage" now extend ventrally as far as van Wijhe's second somite. The second region of cell migration is at this stage sharply confined to encephalomere V. Behind this a disassociation of neural-crest cells has begun in the region of encephalomere VI, but no migration has taken place. From an examination of later stages, the cells proliferated from the region of encephalomere V are easily proved to pass ventrally into the hyoid arch, and to form the ganglionic Anlage of the acustico-facialis. From a study of mitotic cells and from the grouping of cells one is led to believe that the greatest cell proliferation takes place in the posterior part of this neuromere.

It is to be noticed that the advancing ventral end of the ganglionic Anlage extends toward the cleft between van Wijhe's third and fourth somite. Also that cell processes from each of these somites now extend toward the ganglionic Anlage.

When the embryo possesses 19 or 20 somites (Plate **3**, Fig. 9) the "Trigeminus Anlage" shows a differentiation into an anterior smaller portion, which passes in front of the midbrain vesicle toward the optic evagination, and a posterior larger portion, which extends ventrally into the mandibular arch, just beneath the superficial ectoderm and external to the second somite. I am inclined to believe that this division of the Anlage is partly due to the enlargement of the vesicle of the midbrain, since frontal sections show that the lateral wall of the midbrain lies very close to the ectoderm. It is evident that the neural-crest cells migrate around the most expanded portion of the vesicle, so that they come to lie in the regions of constriction anterior and posterior to the dilated vesicle. They migrate, as it were, into the spaces where there is room for them. The cells of these two portions are in continuity dorsally, as in the previous stage. As a result of the expansion of the dorsal wall of the neural tube in the region of encephalomere III, the cells of the neural crest are laterally displaced in this region, so that they appear in optical sagittal section (Fig. 9) to have taken a more ventral position. Mitrophanow ('93) has given the name "le groupe nerveux anterieur" to the anterior smaller portion of the trigeminus Anlage, and states that "dans la plupart des cas, ce groupe est peu séparé" (i. e. from the "groupe du nerf trijumeau"). Coggi ('95) finds that in Torpedo this anterior portion of the trigeminus Anlage arises as a paired structure, the lateral halves of which secondarily unite in the mid-dorsal line; Coggi, however, agrees with Mitrophanow that this anterior part of the trigeminus is at first distinct from the posterior larger portion. In S. acanthias, however, I find that both anterior and posterior parts form at first a continuous neural ridge, which lies dorsal to the midbrain vesicle. Only in later stages does the anterior portion become separated as the so called thalamic nerve. At the stage with 19 or 20 somites the cells proliferated from encephalomere V extend somewhat farther ventrad toward the hyoid arch than in the preceding stage, and at the same time a proliferation of cells from the mesoderm extends dorsad to meet them. The mesodermal cells migrate from both sides of the constriction between van Wijhe's second and third somites, and from them extends a cellular process toward the ganglionic Anlage.[1]

The conditions remain practically unchanged in a stage with 21 or 22 somites (Plate **3**, Fig. 10). The anterior and posterior portions of the trigeminus Anlage now extend into the region ventral to the midbrain vesicle, and are about to unite with each other. The cells in the region of encephalomere III have undergone a still greater lateral displacement, from which one may infer that cells are no longer proliferated from the neural crest of this encephalomere. It is seen that the cells of the acustico-facialis are now united with the cellular process from the mesoderm.[1] This process may be traced dorsally to a point outside of the ganglionic Anlage, i. e. between it and the superficial ectoderm. The future course of the nerve is along the line of the process. Between this and the next succeeding stage, which is represented in Figure 11, the trigeminus Anlage undergoes a considerable change. The anterior (thalamic) and posterior (trigeminal) portions having fused ventrally below the lateral midbrain swelling, now extend ventrad as a continuous sheet with two ventral processes, one reaching into the mandibular arch and the other to a point below the eye vesicle. The anterior (thalamic) portion has assumed a more compact appearance, and extends from the region of the constriction between forebrain and midbrain, both ventrad, to a point above and behind the eye vesicle, — where, as already stated, it meets the anterior prolongation of the trigeminus portion, — and anteriad to a point in front (dorsad) of the eye vesicle. The acustico-facialis Anlage now extends into the hyoid arch, *its position being clearly inter-somitic.* Posteriorly, in the region of encephalomere VI, and to a considerable extent behind this, the cells of the neural crest have begun their ventral migration. At this time, then, a continuous neural ridge or crest extends from the anterior boundary of encephalomere V backward into the region of the spinal cord. In cleared specimens and in parasagittal sections the neural crest cells seem discontinuous in the region of constrictions between encephalomeres IV, V, and VI. Both Rabl ('92) and Hoffmann ('94) have held that the pre-auditory portion of the neural crest is discontinuous with the post-auditory portion, and Rabl considers this another proof that the pre-auditory region is one "sui generis." On the other hand, Dohrn ('90) and Mitrophanow ('93) have stated, like the present author, that they find the crest continuous in the two regions.

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[1] I have been unable to determine that these mesodermic cells participate in the formation of the Anlage of the nerve. It appears to me, however, that such a response on the part of the somites to the development of a nerve Anlage is a fact which cannot be ignored in dealing with the question of nerve development. See also similar evidence in the description of the development of the trochlearis and oculomotorius.

A well marked proliferation of cells seems to take place in the region of encephalomere VI. These cells may be traced continuously into later stages, until they enter the first branchial arch and form the Anlage of the glossopharyngeus. Since previous investigators, with the exception of Herrick and Broman (see Table II., p. 152), have stated that the glossopharyngeus is related to hindbrain neuromere VII,[2] it seems well to call attention to the fact that the cells of the ganglionic Anlage of this nerve

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[1] Is this mesodermal process the median branch of Kupffer's typical segmental *nerve?* Its relation to the mesoderm leads me to believe that this is the case. It soon disappears, as stated by Kupffer ('91).

[2] Miss Platt ('89) stated that the glossopharyngeus is connected with the posterior constriction of encephalomere VI.

are proliferated from the region of encephalomere VI, the greatest proliferation occurring, however, as in the case of encephalomere V, in the posterior part of the encephalomere. No previous observer has stated that the cells of the ganglionic Anlage of the ninth nerve are proliferated from encephalomere VI. However, that previous observers have seen the proliferation of cells from this encephalomere is possibly shown by the fact that both Shipley ('87) and Kupffer ('94) have found in Petromyzon, between the Anlagen of the 7th and 9th nerves, a "weak primitive acusticus, which soon vanishes." Hoffmann ('94) stated that in Acanthias embryos with 32 to 35 somites, a new outgrowth appears between the facialis and the glossopharyngeus, which to all appearance is a rudimentary and early aborting segmental nerve. Although Hoffmann published no figures, I infer from his description that this outgrowth, or rudimentary nerve, is that portion of the neural ridge which is proliferated from the region of encephalomere VI. I am at least able to say positively that no other outgrowth of cells takes place just posterior to the Anlage of the acustico-facialis. In the phenomena presented by this outgrowth Hoffmann finds the chief support for his contention that the Anlagen of cranial nerves arise as paired segmental outpocketings of the neural tube, corresponding to, or comparable with, the outgrowth of the eye vesicles. He figures diagrammatically the outgrowth of the neural crest in the region of the glossopharyngeus Anlage as an outpocketing of the dorsal wall of the neural tube possessing a lumen continuous with that of the tube. At no time do I find evidence of a lumen between the neural-crest cells, although in later stages the nuclei in the VII and IX ganglionic Anlagen tend to take a peripheral position.

At a stage with 26 or 27 somites (Plate **3**, Fig. 12) the thalamic portion of the trigeminus Anlage is no longer continuous dorsally with the posterior portion of the Anlage, the cells of which come to lie in the region of constriction between midbrain and hindbrain. The thalamic portion extends from the constriction between primary forebrain and midbrain toward the eye vesicle, just behind which it unites with a line of cells, ectodermal in origin, which extends along the dorsal border of the eye close to the superficial ectoderm. Some of the cells of the trigeminus Anlage now extend into the mandibular arch, and have there come to surround the mandibular mesoderm.

A displacement of the cells of the Anlage of the acustico-facialis and of the glossopharyngeus has begun at this stage. This is clearly to be accounted for by the invagination of the auditory epithelium, which is now beginning opposite encephalomere VI. In parasagittal sections the Anlage of the glossopharyngeus appears clearly distinct from that of the vagus, while in the median plane they are seen to be continuous portions of the neural crest.

When the embryo has 28 to 30 somites (Fig. 13) the conditions, so far as the trigeminus is concerned, are practically unchanged. Neural-crest cells still persist in the regions of constriction between the primary brain vesicles. Thus, three strands of neural-crest cells are seen to lie in the region of constriction between the brain vesicles, just as they do in the trunk between the myelomeres. The ganglionic Anlage of the acustico-facialis, which had fused with the thickened auditory epithelium in the early stages of its development, now, as the nerve Anlage recedes from the ectoderm, retains this connection, forming thus the Anlage of the acusticus. The acusticus therefore in its development and relations resembles a *ramus dorsalis* of a cranial nerve.

The cells of the glossopharyngeus have been further displaced. In all the specimens of this stage which I have examined, two distal portions of the nerve Anlage may be distinguished. The fate of the posterior of these is unknown to me. The cells of the anterior portion pass ventrally into the third visceral arch, and are related to the constriction between van Wijhe's somites 4 and 5. In precisely the same way the Anlage of the seventh nerve occupies the cleft between the third and fourth somites. The advancing ganglionic Anlagen pass close to the superficial ectoderm in the plane of the constrictions between the somites. Similarly the Urvagus Anlage meets the mesoderm at the posterior cleft of the fifth somite. This fact seems to me to be of some importance in considering the question whether the branchial nerves are somitic or intersomitic in position, and to warrant the conclusion that the cranial nerves resemble the dorsal nerves of Amphioxus in being intersomitic, as well as in other respects. At a stage with 33 or 34 somites (Plate **3**, Fig. 14) the trigeminus Anlage retains connection with the mid-dorsal line of the neural tube in only two restricted regions, anteriorly by the "thalamic" portion, and posteriorly (in the region of the constriction between midbrain and hindbrain) by a strand of cells to which Miss Platt has given the name "primary trochlearis." Posteriorly the cells of the trigeminus Anlage are grouped into a somewhat thickened mass opposite the posterior part of encephalomere III, the first indication of the differentiation of the Gasserian ganglion. The Anlagen of the acustico-facialis and the glossopharyngeus have become farther separated by the invagination of the auditory epithelium, the displacement affecting the cells of the glossopharyngeus so much that they now lie opposite encephalomere VII. The two nerve Anlagen, however, usually remain connected with each other dorsally by a thin cellular strand. This strand is wanting in some cases, or may be present on one side of the embryo only. Dohrn ('90) has also stated that the separation of the seventh and ninth nerves is due to the crowding caused by the ear capsule, and he held that the connecting strand of cells was evidence of the original continuity of the neural crest on the dorsal side of the ear. Behind the glossopharyngeus the neural crest extends in unbroken continuity into the trunk, but only its anterior portion, which forms the ganglionic Anlage of the Urvagus, extends ventrally between the mesoderm of the side plates and the superficial ectoderm into the region of the pharynx.

In embryos with 38 or 39 somites (Plate **3**, Fig. 15) the thalamic portion still extends as a compact cellular cord from the region of constriction between forebrain and midbrain to a point above the eye, where it unites with the line of ectodermal cells which in later stages forms the ophthalmicus profundus trigemini. This nerve, because of its relations with the trigeminus, "primary trochlearis," and "thalamic" nerves, is regarded by Marshall ('82) and Miss Platt ('91) as a commissural nerve connecting the three nerves mentioned. It has also been regarded as an independent nerve (van Wijhe, '82, M. Fürbringer, '97), and as a ramus dorsalis either of the trigeminus or the oculomotorius. The acusticofacialis Anlage, opposite encephalomere V, is still in continuity with that of the glossopharyngeus by means of a cellular cord dorsal to the auditory invagination, while the cells of the glossopharyngeus and vagus Anlagen no longer appear to be continuous dorsally, as they were in the previous stage.

At a stage of development when the embryo possesses 42 to 44 somites (Plate **3**, Fig. 16), and when two visceral clefts are formed, both the thalamic and trochlear portions of the trigeminus Anlage are much reduced. In an embryo with 48 somites the thalamic portion consists of a strand or cord of cells which extends dorsally from the ophthalmicus profundus, at a point just above the eyestalk, toward the region of constriction between primary forebrain and midbrain, where the two cellular strands coming from opposite sides of the head unite above the wall of the brain. Because of this union, Coggi ('95) has considered this portion of the trigeminus Anlage as a connective "nerve," uniting the *lateral halves* of the ophthalmicus profundus. Its position in Torpedo, according to Coggi, is anterior to the thalamencephalon. If Coggi is correct, its position in Torpedo is clearly different from that in S. acanthias. Coggi's account differs, however, from that of Dohrn ('90^a), who found its relations in Torpedo to be similar to those described by Miss Platt ('91) for S. acanthias. The relations of the acustico-facialis and glossopharyngeus remain unchanged. For a long time cellular strands persist, showing the primitive relation of these nerves to the constrictions between the encephalomeres IV, V, and VI, respectively.

Some important changes in the relations of the neural-crest cells appear in the next (48-somite) stage, and are shown in Plate **3**, Figure 17. For the first time, we find "fibrillar" connections of the trigeminus Anlage with the neural tube. Protoplasmic or fibrillar processes extend from the cells which lie opposite the constriction between encephalomeres III and IV toward both encephalomeres. It has been stated by some investigators (Miss Platt, '91, Locy, '95), that this nerve has its origin from the constriction between the neuromeres. Two main roots are differentiated later, an anterior, in relation with encephalomere III (the "portio minor"), and a posterior, in relation with encephalomere IV (the "portio major"). The nearness of the ganglion cells to the brain wall renders it impossible for me to determine in which direction, whether toward the brain or toward the ganglion, the fibres are first developed. The two chief roots of the trigeminus have been described for other Vertebrates.

The thalamic and trochlearis portions of the trigeminus Anlage are now much reduced in size, each retaining connection with the rest of the nerve fundament by means of an attenuated protoplasmic fibre. The acustico-facialis Anlage has assumed fibrillar connection with encephalomere V, with which it remains connected until the encephalomere disappears. Marshall and Spencer ('81, p. 481, '86, p. 100) have stated that in Scyllium "there is an important difference between the fifth and seventh nerves, inasmuch as in the former the primary root is lost and the secondary alone retained, whilst in the latter both primary and secondary roots are retained up to stage N, and indeed . . . throughout life. The difference between the roots of the fifth and seventh nerves just noticed does not occur in the chick." They also state that in early stages in Scyllium embryos the fifth nerve arises from the brain by three distinct roots, but that in later stages only two roots are found. Their distinction between primary and secondary nerve "roots" is obviously unnecessary, since the only true "roots" are the so called secondary ones. Before these are established we have to do with neural-crest cells, some of which have been shown to be non-nervous in function, and to contribute to the mesenchyma of the head.[1] The ear capsule now lies with only its anterior portion opposite encephalomere VI. Behind the ear capsule and opposite the posterior portion of encephalomere VII lie the cells of the glossopharyngeus, as yet without fibrillar connections with the neural tube. Behind the glossopharyngeus and now separated from it lie the cells of the vagus, extending ventrally as a broad sheet between the mesoderm and ectoderm into the region of the pharynx, where the Anlage becomes segmented by the formation of the visceral clefts. The trochlear and thalamic portions of the trigeminus soon disappear without assuming fibrillar relation with the neural tube.

At a stage with 52 somites, when the embryo is about 8 mm. in length, the thalamic portion remains as a group of cells lying in the constriction between the forebrain and midbrain vesicles (Plate **4**, Fig. 18), but without connection with the ophthalmicus profundus. It very soon disappears entirely, and I think probably contributes to the loose mesenchyma of this region. In precisely the same way the disassociation of cells of the trochlear portion takes place, scattered clumps of cells indicating its previous extent. The Gasserian ganglion and the ganglion of the ramus ophthalmicus profundus (mesocephalic ganglion) are both clearly differentiated. Three branches of the fifth nerve may now be distinguished, viz. the two sensor branches, r. ophth. profundus and r. maxillaris (inframaxillaris[2] Dohrn), and the mixed mandibular branch. Nerve relations to the neural tube remain the same as in the previous stage.

d. DEVELOPMENT OF THE

1. OCULOMOTORIUS.

By the time the embryo has reached the length of 8 mm. (52 somites), the oculomotorius has however appeared as a fibrillar process from the base of the midbrain (encephalomere II, Figures F to H), arising as processes from neuroblast cells in the ventral horn of this encephalomere. Since this nerve throws light on the morphology of the premandibular somite, whose musculature it innervates, its development is of great interest and has been studied by many investigators; viz. Marshall ('81), Rabl ('89), Dohrn ('91), Platt ('91), Mitrophanow ('93), and Sedgwick ('94). Neither Marshall ('81) nor Rabl ('89) saw the early stages of its development, and their conclusions are therefore purely theoretical. Both agree in considering the nerve a derivative of neural-crest cells. Rabl ('89, p. 221) thinks he has some right to bring this portion of the neural crest into genetic connection with these nerves, since the course of the third and fourth nerves in later stages corresponds with a portion of the trigeminus Anlage, which I infer from his description to be the "trochlear" portion. He adds, "Ferner darf ich aus einer Reihe von Beobachtungen, die ich nicht bloss an Selachiern, sondern auch an Vögeln und Säugethieren angestellt habe, schliessen, dass die Oculomotoriuswurzel, die nach dem gesagten Anfangs ebenso wie die des Trochlearis aus der dorsalen Kante des Mittelhirns austreten musste, aus dieser Lage allmählich durch die Ausbildung der Pedunculusbahnen verdrängt und an die ventrale Seite verschoben wird."

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[1] Kastschenko ('88), Goronowitsch ('92), Miss Platt ('93).

[2] This is, I believe, the nerve which in Ceratodus van Wijhe ('82) named ramus maxillaris superior, which in Amphibia Strong ('95) called accessory branch of the fifth, and Miss Platt ('96) r. buccalis profundus V.

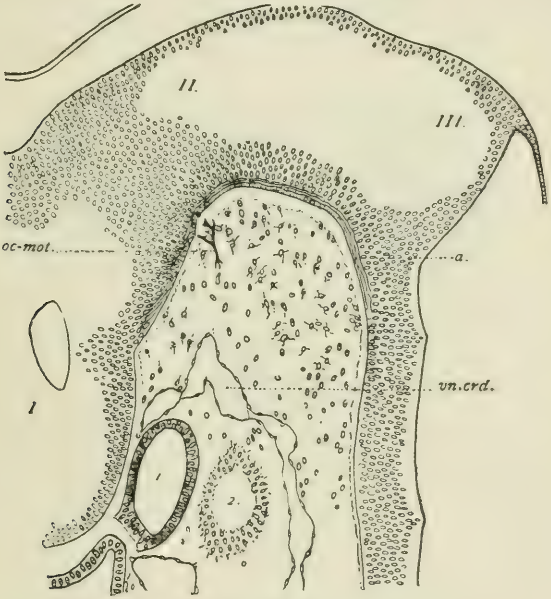

FIGURE F.

FIG. F. Left face of a parasagittal section through the left half of an embryo with 52 somites, showing the relations of the oculomotorius to encephalomere II at this stage. × 50. *I, II, III*, first, second, and third encephalomeres; 1, 2, van Wijhe's first and second head cavities; *a*, ventral fibre tract; *oc-mot.*, oculomotorius; *vn. crd.*, anterior cardinal vein.

More theoretical and farther from the truth Rabl could scarcely be, yet several investigators have in essential respects confirmed his theory, that the oculomotorius is a derivative of the neural crest. Dohrn's ('91) observations, however, differ fundamentally from those of his predecessors. He sees the beginnings of the oculomotorius in embryos intermediate between Balfour's stages I and K. At first cells in the base of the brain assume a more transparent appearance, and later migrate into the "Randschleier," where they send out processes which unite in a network just outside the base of the brain to form the stem of the nerve. Immediately at the beginning of the outflow of the plasma cells are seen half in and half out of the wall of the tube, and later, but before the oculomotorius has any connection with the mesocephalic ganglion, large deeply staining nuclei are seen in the protoplasmic network which forms the root of the nerve. Dohrn does not lay great stress on the fact that these nuclei are larger than those of the surrounding mesenchyma cells, but from the fact that similar nuclei lie nearer the medullary wall, from which they appear to emerge in increasing numbers during the course of development, he holds the opinion to be permissible, that the nuclei of the early network are emerged medullary elements, and not mesoderm cells which press close to the medullary

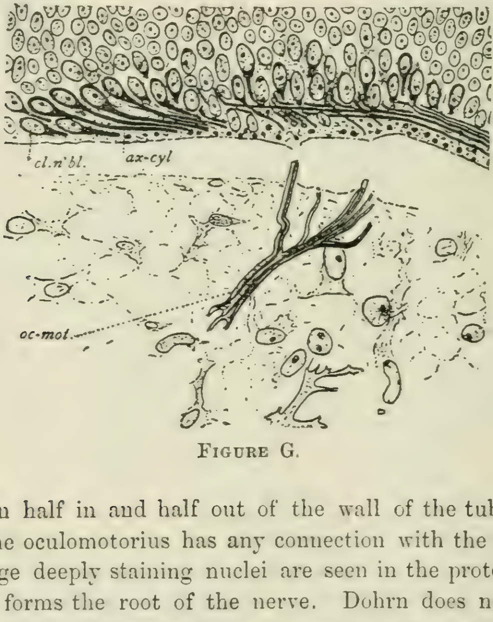

FIGURE G.

FIG. G. A portion of the same section as that shown in Figure F. × 240. The fibrillar nature of the oculomotorius is clearly shown. *ax-cyl.*, axis cylinder process; *cl. n'bl.*, neuroblast cell; *oc-mot.*, oculomotorius.

wall. Dohrn considers it as the *punctum saliens* of the evidence given by him, that ganglion cells and ganglia which may be traced to the adult are to be found in the course of the oculomotorius before this comes into connection with the mesocephalic ganglion, and concludes that such ganglion cells can have had no other source than the ventral horn of the midbrain. He thus takes the view of Balfour, Marshall, Kupffer, and others, that this ventral nerve is formed as a chain of medullary cells, in opposition to the views of His ('89), Kölliker ('92), von Lenhossék ('92), and others, that ventral nerves are formed from *processes* of "neuroblast" cells in the ventral horn of the medullary tube.

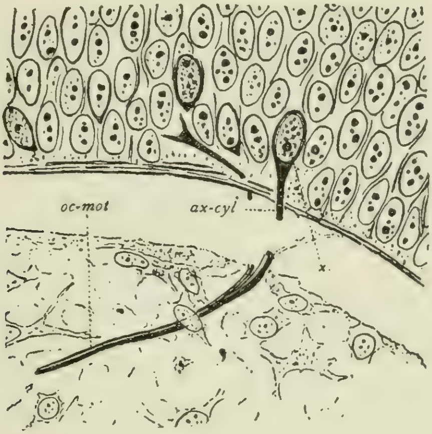

FIGURE H.

Miss Platt ('91) comes to fundamentally different conclusions from those of Dohrn ('91). She finds that the oculomotorius appears first as a single cell proliferated from the mesocephalic (ciliary) ganglion toward the base of the midbrain, with which it at first has no connection. Observations on Squalus, Raja, Pristiurus, and Torpedo convince her that the oculomotorius develops after the type of a sensor nerve [?] by a proliferation of ganglion cells toward the brain wall. Mitrophanow's ('93)

FIG. H. Left face of a parasagittal section through the right half of the same embryo as that represented in Figures F and G, showing the oculomotorius in an early stage of development (52 somites). × 447. The relation of the nerve fibre with an axis-cylinder process from the neuroblast cell x seems clear. *ax-cyl.*, axis-cylinder process; *oc-mot.*, oculomotorius; x, neuroblast cell.

observations confirm those of Miss Platt. According to Sedgwick ('94) the third nerve is formed directly from the neural crest as are the dorsal cranial nerves [?], but arises as a differentiation of the reticulum formed by the breaking up of the neural crest, and first makes its appearance as a projection of nuclei from the mesoceplalic ganglion. His observations thus do not essentially differ from those of Miss Platt, their conclusions differing chiefly by reason of difference in theoretical views as to the mode of nerve development. My own evidence differs quite fundamentally from that given by previous investigators, since I find that the nerve develops after the manner described for spinal ventral nerves in Selachii and other Vertebrates, as an axis-cylinder process from "neuroblast" cells in the ventral horn of the midbrain. At the earliest stage in which I have been able to detect the oculomotorius the extent of its development and its relationships are such as are shown in Figures F to H, which represent sagittal sections of a Squalus embryo with 52 somites (approximately 8 mm. long). At this stage the thalamencephalon is just becoming differentiated from the primary forebrain (encephalomere I). The identification of the fibrillar process as the oculomotorius is made easy by a comparison of its point of attachment, of the direction of its long axis, and of its histological appearance with those of an embryo with 54 somites, where the oculomotorius is already connected with the mesocephalic ganglion. Under higher powers of the microscope the nerve appears as a deeply staining, highly refractive process, clearly distinguishable by these characteristics from the granular and faintly staining processes of the mesenchyma cells at the base of the midbrain. Owing to a shrinkage, which however appears in very few of the specimens killed by the fixing agent used (vom Rath's fluid) and always most markedly in the region ventral to the midbrain, the mesenchyma cells and the roots of attachment of the nerve have broken away from the base of the brain. Since, however, similar deeply staining processes are seen to extend from cells in the ventral horn of the medullary tube towards the points where the roots may be supposed to have once united with the wall of the brain, the inference seems warranted that the nerve is made up of the processes of these cells. The latter show the characteristics described by His ('89) for the neuroblasts of the spinal cord, viz. a highly chromatic nucleus surrounded by a thin, very deeply staining protoplasmic ring, which is prolonged into the axis-cylinder process. The precipitation of osmium serves to render the processes quite opaque and easily traceable among the remaining, as yet undifferentiated, cells of the medullary wall, and to make it possible to determine that other processes, instead of leaving the medullary wall, extend posteriorly in the wall and parallel with it to form the ventral fibre tract. The nerve process (Figure G) shows a differentiation in its distal portion into two deeply staining fibrils surrounded by more faintly staining plasma, the two fibrils dividing distally into three, which enter the fine processes with which the nerve ends. The nerve process on the other side of the same embryo (Figure H) does not, however, show this same evidence of histological differentiation. Here the nerve appears as a highly refractive fibril, and, while having a greater extent than that of its mate of the opposite side, is composed, except at its root, of a single undivided fibril. The connection of this fibril with the axis-cylinder process from a neuroblast cell in the ventral horn seems indisputable, since this passes directly through the limiting membrane at the base of the brain wall, and projects into the shrinkage space directly opposite the chief root of the nerve, as is shown at *ax-cyl.* I have no evidence to offer, such as that stated by His ('88, '89), for Mammals and other Vertebrates, of a migration of the neuroblasts from the "inner layer" of medullary cells, nor do I find any evidence of migration of cells from the neural tube, as stated by Dohrn ('91). I find at this stage neither nuclei connected with the roots of the nerve outside the neural tube, nor such as are half in and half out of the tube.

The connection of the oculomotorius with cells of the mesocephalic ganglion is attained very quickly, and in embryos of 54 or 55 somites has already taken place. At this stage of development, as seen in embryos fixed with the corrosive sublimate-acetic mixture (Davidoff's fluid), the nerve appears (Plate 8, Fig. 58) as a *cellular* strand, which extends from the inner side of the mesocephalic ganglion toward the ventral wall of the midbrain, with which the nerve unites by at least two main roots. To detect the proximal roots as well as the relations of these with medullary cells, sagittal sections are much more favorable than frontal, since the nerve roots are situated one behind the other.[1] The fact that the nerve is several cells in thickness near the ganglion, while its calibre diminishes as it passes toward the brain wall, would naturally, if one were unacquainted with the conditions shown in the embryo of 52 somites, lead to the inference that the growth of this nerve takes place from the ganglion toward the brain (*vide* Miss Platt, '91, Mitrophanow,

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[1] Also, for the reason already stated by His ('88^b, p. 344) for spinal ventral nerves, that "die Wurzelbündel treten in grösseren Abständen aus dem Ruckenmark hervor. Jedes Bündel bezieht seine Fasern aus einem entsprechend breiten Bezirk des Rückenmarks. Die Sammlung derselben erfolgt zum Theil noch innerhalb des Markes, zum Theil erst in der Leibeswand."

'93, Sedgwick, '94). It is interesting to compare the phenomena thus observed in specimens prepared by the Davidoff method with those prepared by the vom Rath method, since the latter clearly differentiates the nerve fibrils, and gives the clue as to the meaning of the cells proliferated from the mesocephalic ganglion. Figure I is drawn from a sagittal section of an embryo with 55 somites killed by the vom Rath method, and fortunately so oriented as to show the oculomotorius in its course from the inner side of the mesocephalic ganglion to a point very near the brain wall. The nerve itself is composed of three deeply impregnated fibrils, which near the brain wall are closely united to one another, while peripherally they become separated. Two lightly staining cells with granular protoplasm lie closely adherent to the nerve, and with low powers are indistinguishable from it. Others appear in the process of migration from the mesocephalic ganglion to assume similar relation. Whether these cells become elements of the oculomotorius ganglion, which would thus conform in its mode of development to the type of a sympathetic ganglion,[1] or whether they form the nuclei of Schwann's sheath, I am not at present in a position to state, since I have not been able to trace their fate. It is of course possible that they contribute to both ganglion and sheath. Whether cells from the mesenchyma in this region contribute to both of these ends, seems to me a question of not great morphological importance, since in my opinion these cells are in great measure, if not entirely, derivatives from the neural crest, and thus *ectodermal*, not mesodermal, in origin. From the evidence thus stated it is seen that the oculomotorius must be

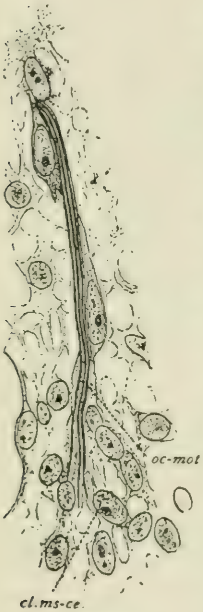

FIGURE I.

[1] Many investigators (Rüdinger, Arnold, Gegenbaur, Schwalbe, Hoffmann, Onodi, van Wijhe, Dohrn, Beard, Ewart) have, on histological and embryological grounds, agreed that this ganglion belongs to the sympathetic system.

FIG. I. Sagittal section of a Squalus embryo with 55 somites, showing the oculomotorius in its course from the mesocephalic ganglion toward the brain. × 477. The fibrillar nerve and the peripheral nuclei may easily be distinguished. *cl. ms-ce.*, migratory cell from the mesocephalic ganglion; *oc-mot.*, fibres of the oculomotorius.

regarded as from the earliest stages of development a fibrillar nerve formed by axis-cylinder processes of medullary cells, and that it is no more to be regarded as a *cellular* process or *cellular* nerve in its earlier than in its later stages. The unfavorableness for purposes of nerve study of material killed, with the fixing agents commonly used, has been the chief cause which has kept us so long from the true understanding of the method of the development of the oculomotorius in Selachii. I was at first disposed to consider as of some morphological importance the fact that in stages of development before the appearance of the oculomotorius a process extends from the mesocephalic ganglion to the premandibular somite (Plate **8**, Fig. 61). Its earlier appearance precluding the view that this process has connection with the oculomotorius, I concluded that it furnishes us with evidence of a primitive relation of the ramus opthalmicus profundus with this somite (Plate **8**, Fig. 61). The observations of J. Müller in 1840, P. Fürbringer ('75), Price ('96), and Max Fürbringer ('97), have established that this nerve possesses motor fibres in the Myxinoids, confirming van Wijhe's view of its segmental value. I am, however, not inclined to lay stress on the fact mentioned above as confirmatory of this view, since in later stages (65 somites) I also find a similar process, apparently in connection with the "anterior cavity" (Plate **4**, Fig. 19).[1]

At a stage with 65 somites (10 mm.) the relations of the trigeminus are unchanged (compare Plate **4**, Fig. 19). The r. ophthalmicus profundus trigemini is well differentiated, and shows a marked fibrillar structure, especially clear in embryos killed with vom Rath's fluid. The nuclei seen along the trunk of the nerve are distinctly peripheral in relation to the nerve fibres. The facialis nerve (VII) now possesses four branches, viz. the sensor acusticus branch, connected with the median and ventral side of the otic capsule; the mixed hyoid nerve, innervating the muscles and skin of the 2d visceral (hyoid) arch; the r. ophthalmicus superficialis VII (ophthalmic branch of the 2d trigeminal root of older anatomists), whose sensor fibres develop in close connection with the skin along what in the head corresponds with the dorso-lateral line of the trunk; and the r. buccalis VII (incorrectly called supramaxillaris V by Wiedersheim), developing along the medio-lateral line of the head.

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[1] Allis ('97, p. 742) also describes in Amia calva a small and apparently degenerating nerve in connection with the ganglion of the profundus. He however, on grounds of the topographical relation of the eye-muscle nerves (III and IV), regards this nerve as homologous with the ophthalmicus profundus trigemini.

The glossopharyngeus is now in fibrillar connection with the lateral walls of the neural tube at a point behind encephalomere VII. The fibres from the ganglion cells of the vagus enter the neural tube at a point somewhat behind the point of origin of the glossopharyngeus. The cells of the two nerve Anlagen, however, still appear continuous. Posteriorly, and at the same level as the origin of the roots of nerves IX and X, the neural-crest cells appear as a commissure (*coms. d.*) connecting the vagus Anlage with the ganglia of the dorsal spinal nerves Ventrally the vagus divides into four mixed (post trematic) branches, each of which innervates the skin and musculature of a visceral arch, and posteriorly is continued beneath the skin as the ramus lateralis vagi along the medio-lateral line.[1]

At this stage, I find the first evidence of the olfactory nerve (I) in the form of connecting strands or fibres between the anterior lateral wall of the forebrain (prosencephalon) and the thickened lateral epithelium of the olfactory plate. The connection between the median portion of the "Riechplatte" and the brain wall (neuropore) has disappeared at a somewhat earlier period (8–9 mm.). According to Marshall ('78) and Beard ('85) the olfactory nerve develops, as do the other dorsal cranial nerves, from cells of the neural crest, and is therefore regarded by them as a nerve morphologically comparable with the dorsal cranial nerves. The evidence given by van Wijhe ('86^a) and Hoffmann ('96), however, serves in the opinion of these investigators to render this view improbable. Van Wijhe ('86^a, p. 680) states that "das Riechorgan und der Nerv entstehen beide aus dem vorderen Neuroporus. Der Olfactorius entwickelt sich nicht aus der Nervenleiste, denn er tritt in einer Periode auf, wann dieselbe im Kopfe schon längst geschwunden ist; auch ist er von Anfang an mit der Haut in Verbindung und unterscheidet sich durch diese zwei Merkmale von allen übrigen dorsalen Nervenwurzeln. Der Riechnerv entsteht also erst nach dem Acranienstadium und in Uebereinstimmung damit ist seine Abwesenheit beim Amphioxus."

Confirmatory of this view is the evidence given by Hoffmann ('96, p. 272) that "der Riechnerv fehlt [in Squalus] aber bis zu diesem Entwicklungsstadium [10–12 mm.] noch vollständig und erst bei Embryonen, welche eine Länge von 13½–14 mm. erreicht haben, beginnt er sich anzulegen. Bis zu dieser Periode liegt die Riechgrube der Medullarwand immer noch unmittelbar an, dies ist auch jetzt noch grösstentheils der Fall, aber mit ihrem medialen Rand fängt sie jetzt an sich von der Gehirnwand zurückzuziehen, bleibt aber mit ihr durch einen kurzen, dicken Zellstrang kontinuirlich verbunden. Dieser Zellstrang bildet die Anlage des Nervus olfactorius, aber es ist nicht möglich zu sagen, welchen Antheil die Epidermis und welchen das Gehirn an der Anlage der Riechnerven nimmt, denn er entsteht aus dem letzten Rest des kontinuirlichen Zusammenhanges von Epidermis und Medullarwand, welcher von Anfang an bestanden hat."

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[1] Squalus possesses no *dorso*-lateral line nerve corresponding with that of Cyclostomata, Dipnoi, and Ganoidei. I also find no evidence in Squalus such as that found by Miss Platt ('94) in Necturus, to show that there once existed a *ventro*-lateral line in Vertebrates.

His ('89^a) had previously found in the human embryo that the first step in the formation of the olfactory nerve was the migration of mesenchymatous cells between the olfactory plate and wall of the brain. Later the olfactory ganglion is formed by the migration of cells from the lateral walls of the olfactory epithelium. Finally, the olfactory nerve results from the assumption by these cells of a bipolar form and the elongation of the poles both centripetally and centrifugally to form fibrillar connection with brain and olfactory pits.

My own observations concerning the development of the olfactorius are as yet incomplete, and I am not able to add much to the evidence which has been given. In agreement with Hoffmann ('96) I find that, as the olfactory plate and the brain wall separate, they retain connection with each other by faintly staining fibrils in the region of the future olfactory pits. Whether these fibrils enter into the formation of the definitive olfactorius I am not able to state, and the observations of Hoffmann appear to me insufficient to establish this fact. My results and those of Hoffmann do not agree; for he finds in embryos of 16 mm., and still more clearly in embryos of 18–20 mm., that *mesenchymatous* tissue "schiebt sich von allen Seiten zwischen Medullarwand und basale Nasengrubewand ein, und in demselben Grade als beide sich entfernen, nimmt natürlich der Riechnerv an Länge zu." I infer this mesenchymatous tissue to be the same as that which Hoffmann previously states to be derived from the "anterior head cavities." My observations, however, lead me to agree with Marshall ('78), that the cells which appear between the nasal pit and the brain wall, as these separate, are neural-crest cells. Van Wijhe may be technically correct in stating that the neural crest has disappeared in the region of the forebrain at the time when the olfactory nerve is established; but it is certainly not true that the neural-crest *cells* in the region of the forebrain have done so at this stage. They persist in the region of the forebrain which lies opposite and anterior to the optic vesicle, and in my opinion are the cells which migrate between olfactory pit and brain wall as these separate from each other. I regret that I am not yet in position to describe the later differentiation of these cells, but it appears to me not improbable that they enter into the Anlage of the olfactorius. The evidence given by many histologists, from Schulze to Retzius, establishes the ganglionic character of the olfactorius; while the evidence presented by His ('89[a]) appears confirmatory of the view of Beard, that the olfactory plate is to be regarded as the anterior of the sense organs of the lateral line, since from it are derived, at least in part, the ganglionic cells of the olfactorius. Therefore, if neural-crest cells also entered into the Anlage of this nerve, it must be regarded as homodynamous with the sensor component of a dorsal segmental nerve.

2. Abducens.

Another of the eye-muscle nerves, viz. the abducens, is now (65 somites, 10 mm.) differentiated. (Compare Figs. 20 and 21 with Fig. 19.) The latter nerve has arisen as an outgrowth from neuroblast cells in the ventral horn of encephalomere VII, and its roots retain connection with this encephalomere until the latter disappears. Zimmermann ('91) stated incorrectly that its connection in Squalus is with the neural segment which corresponds with my encephalomere VI. Dohrn ('90[c]) describes the nerve as having its origin from the neural tube opposite the otic capsule, and between nerves VII and IX. Its position in different Vertebrates seems inconstant. Some investigators (Orr, '87, Waters, '92, and Herrick, '92) have stated that in the forms studied by them it arises from the hindbrain neuromere corresponding with encephalomere IV of my figures. In the chick and swine I have found that its roots are in connection with encephalomere VI, whereas in Necturus its fibres may be traced from the musc. rectus posterior to a point behind the ear, and thus have, as I believe, their origin from a segment of the hindbrain corresponding with encephalomere VII. At least, in this form, as in Squalus, it appears as a post-otic nerve. Dohrn ('91) gave a careful account of the early stages of its development in embryos of various Selachii. He states that the nerve first appears at a stage corresponding with Balfour's stage L, arising by two roots which unite at a short distance from their point of exit from the ventral wall of the neural tube. In Mustelus the roots are more numerous than in the other forms examined, there being as many as six on each side of the brain. The roots are directed backward, as in the case of spinal nerves, but later form a network from which arises the stem of the nerve; this runs forward, parallel to the neural tube, toward van Wijhe's third somite. In later stages the nerve divides into two branches, one passing along the inner side of the somite, and the other along the outer side. At first the nerve root, which appears as a plasma outflow from the neural tube, is of the thickness of one, or at most two, medullary cells. Later the roots increase in thickness, apparently by the continued outgrowth of plasma from the neural tube, as well as by the migration of cells from the ventral horn of the medulla. The larger size and different staining qualities of the medullary cells enabled him to distinguish them from the mesodermal cells in their vicinity. Such (medullary) cells are often found with a part of the nucleus within and a part without the medullary wall. This outflow (migration) of medullary cells takes place also in later stages after the white substance has become quite thick on the side wall of the neural tube.[1]

My observations upon the development of the abducens differ from those of Dohrn, as in the case of the oculomotorius, inasmuch as I find the nerve to arise from axis cylinder processes of neuroblasts in the ventral horn of the medulla, and therefore to resemble in its mode of development that of a ventral spinal nerve, as stated by His ('89). At the earliest stage which I have been able to detect the abducens, it possesses but a single root, formed by the processes of several neuroblasts, as is represented in Figure J. The union of these takes place just outside the medullary wall, yet peripherally the nerve appears as a single process with deeply staining axis and a more lightly stained sheath. I find neither at this stage nor in later stages any convincing evidence of a migration of the neuroblast cells from the wall of the neural tube. In later stages of development sections show that *the nuclei seen along the course of the nerve are distinctly peripheral in relation to its fibres.* Even the phenomena presented in sections of embryos fixed with corrosive-sublimate acetic, such as are represented in Figures 62–65 (Plate **9**), warrant in my judgment only the inference that the nuclei of the nerve are peripheral, as held by Miss Platt ('91). The darker appearance of the nuclei lying upon the nerve results more from the opaqueness of the nerve than from any peculiar staining properties of the nuclei. During development the number of roots in the nerve increases from one to three or four, the number being variable even upon the two sides of the same embryo. The method of development of the secondary roots is the same as that described for the primary one, viz. as processes from neuroblast cells in the ventral horn. By following the fibres of the roots in the wall of the brain, it is easily ascertained that the motor "nucleus" of the abducens is a very elongated one, as is known to be the case in higher Vertebrates (see Edinger, '96).

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[1] Since Marshall ('81), van Wijhe ('82), and Miss Platt ('91) never saw the early stages of development of the abducens, it is unnecessary to restate their results in this connection.

The study of the development of the abducens is simpler than that of the oculomotorius, since the nerve never comes into relation with a ganglion, and thus resembles the primitive ventral nerves of Amphioxus more than do the ventral spinal nerves. The gradual extension of its fibres through the mesenchymatous tissue at the base of the medulla may therefore be easily followed. It is a matter of some morphological importance, in my opinion, that not all the nerve fibrils extend anteriorly toward the third somite (van Wijhe's), but that in later stages of development, e. g. in embryos with 78–80 somites (Plate **4**, Fig. 20), a nerve fibril is seen to pass from the posterior root of the nerve in a posterior direction toward the myotome of the sixth somite, which has at this stage, however, only a few rudimentary muscle fibres. Miss Platt ('91) likewise has mentioned the fact that this nerve also distributes fibres to mesoderm posterior to the third somite (musc. rectus posterior). In the abducens, therefore, we have to do with a post-otic ventral nerve,

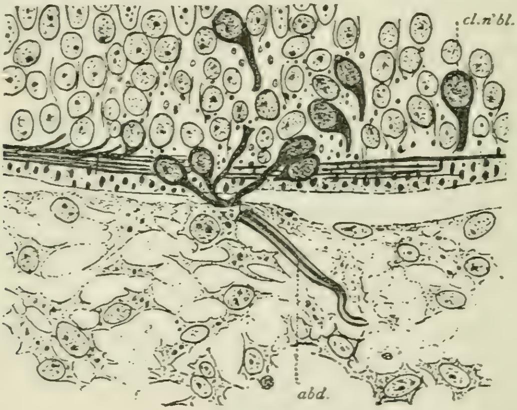

FIGURE J.

FIG. J. Parasagittal section of a Squalus embryo with 60 somites, showing the abducens as a fibril formed by the processes of at least four neuroblast cells. × 447. *abd.*, abducens; *cl. n'bl.*, neuroblast cell.

which develops in precisely the same way as do ventral (medullary) spinal nerves, possesses a much elongated motor nucleus in the ventral horn of the medulla, and innervates pre-otic (possibly also in the embryo post-otic) musculature (musc. rectus posterior). These facts seem significant in dealing with the question of the primitive metameric relations of this nerve.

At a stage when the embryo has a length of 17 mm. (78–80 somites) the ramus opthalmicus superficialis V (Plate **4**, Fig. 20; compare Fig. 21) appears as a fibrillar nerve with peripheral nuclei extending from the Gasserian ganglion just dorsal to the point of exit of the fibres of the r. ophth. profundus V, and passing anteriorly close to the ectoderm below the r. ophthalmicus superficialis VII. The relations of these two ophthalmic nerves are therefore such that they have usually been regarded as of the same morphological value, i. e. as rami cutanei dorsales of nerves V and VII respectively. Yet an interesting relation of protoplasmic processes from the r. ophth. sup. V with the myotome of the second somite, such as is represented in Plate **8**, Figure 60, has been called to my attention by Miss Platt. Since at this stage of development the fibres of the trochlearis have not appeared, the inference would seem warranted that motor impulses may have primitively passed to this myotome (musc. obliquus superior) through the fibres of the r. ophth. sup. V. Such a supposition, however, is greatly diminished in force, and in my opinion rendered untenable, by the fact that in embryos of 19 mm. — therefore before the fibres of the trochlearis are in connection with the m. obliquus superior — the r. ophth. sup. V shows no longer connection with this muscle (Figure K). The fibres of the anterior root (portio minor) of the trigeminus nerve may now be traced from their origin through the Gasserian ganglion into the mandibular arch, where they give off fibres both to the muscles of the arch and to the skin of its anterior and lateral surface. The fibres appear in large part motor. Since this is the only motor branch of the V, it would follow that the posterior root (portio major) includes chiefly, if not entirely, sensor fibres. It would moreover follow that encephalomere III is chiefly, if not wholly, connected with motor fibres, which may be traced forward to a considerable distance in it to the neuroblasts in the lateral horn, with which they are in connection, while encephalomere IV has chiefly sensory fibres in connection with it. Mitrophanow's ('93, p. 178) evidence is, however, considerably at variance with that just stated. He finds that in an embryo Squalus of 18 mm. "la racine du nerf trijumeau est large et se devise en deux parties (Pl. XIV. Fig. 8) dont les fibres sortent du cerveau en formant différents coins et se croisent ensuite au dedans du ganglion Gasseri; de cette manière le ramus ophthalmicus profundus les reçoit de la partie postérieure; le ramus maxillaris, de la postérieure et de l'antérieure; le ramus mandibularis, principalement de la postérieure." Mitrophanow's results are seen to differ markedly from mine as to the relationship of the fibres of the ramus mandibularis. My results, however, agree with those of His ('88^b, p. 365, Tab. II, Fig. 3) for the human embryo. The clear relationship of the motor fibres of the trigeminus with encephalomere III and the visceral part of van Wijhe's second cavity appears to me a matter of considerable morphological importance, and seems to establish the metameric relations of these elements.

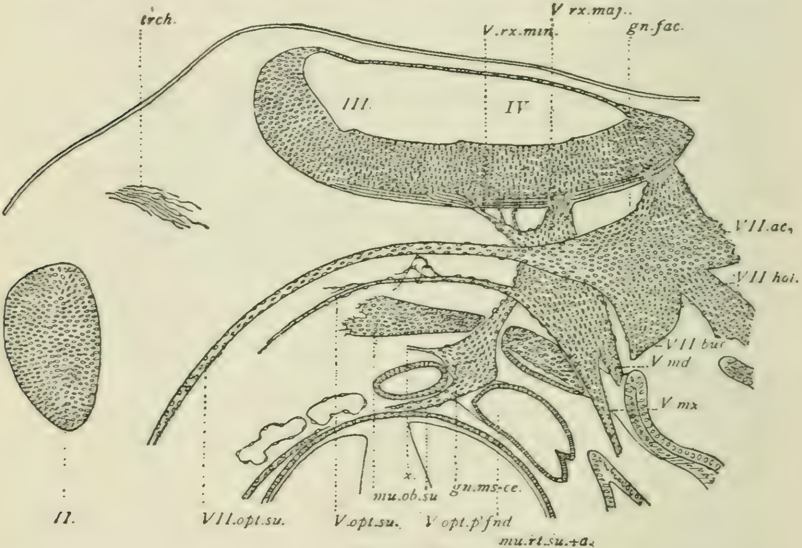

FIGURE K.

FIG. K. Parasagittal section through the left side of a Squalus embryo of 19–20 mm. × 50.

II, *III*, *IV*, second, third, and fourth encephalomeres; *V. md.*, r. mandibularis trig.; *V. mx.*, r. maxillaris trig.; *V. opt. p'fnd.*, r. ophth. profundus trig.; *V. opt. su.*, r. ophth. superficialis trig.; *V. rx. maj.* and *V. rx. min.*, major and minor roots of the trigeminus; *VII. ac.*, r. acustico-facialis; *VII. buc.*, r. buccalis facialis; *VII. hoi.*, r. hyoideus facialis; *VII. opt. su.*, r. ophth. superficialis facialis; *gn. fac.*, ganglion of the facialis nerve; *gn. ms-ce.*, meso-cephalic ganglion still retaining connection with the ectoderm by the process *x*; *mu. ob. su.*, m. obliquus superior; *mu. rt. su. + a.*, musc. recti superior and anterior (1st cavity); *trch.*, trochlearis.

3. Trochlearis.

In an embryo about 21–22 mm. in length (Plate **4**, Fig. 21) the trochlearis, the last cranial nerve differentiated, appears, as stated by Kastschenko ('88, p. 465), in the form of "parallel gehende kernlose und, dem Anschein wenigstens nach, vollständig structurlose Fäden, welche in ihrer ganzen Ausdehnung vom Gehirndach bis zum entsprechenden Muskel verfolgt werden können." The great variety of opinions concerning the morphology of this eye-muscle nerve make interesting the facts of its development. Hoffmann ('89, p. 338), who was the first to study its development, states that in Lacerta one finds, as the Anlage of the trochlearis, "einen ziemlich grossen, zelligen Auswuchs" between midbrain and hindbrain. At certain stages the trochlearis possesses "ein sehr deutliches und zwar ziemlich grosses Ganglion, welches aber frühzeitig wieder vollständig abortirt."[1] In later stages of development the trochlear emerges as "dünner, feinfaseriger Nervenstamm von der oben erwähnten Stelle aus dem Gehirn und wird in seinem weiteren Verlauf bald so schmächtig, dass er nur aus einzelnen, sehr dünnen Fasern besteht." In other reptiles, in birds, and in cartilaginous fishes, Hoffmann was unable to find evidence of this ganglion of the trochlearis. In 1890 and 1891 Dohrn announced that, in early stages of the development of the trochlearis, erratic ganglia, which were evidently products of the neural crest, are found in Selachian embryos in connection with this nerve. Whether these ganglia send fibres into the trochlearis stem, he was not able to determine. In later stages anastomosing fibres appear to connect the trochlearis with the r. ophth. sup. V and VII. Moreover, Froriep ('91) thinks he is able to establish in Torpedo the genetic connection of a pear-shaped ganglion with the trochlearis. From his studies upon Torpedo embryos, he is also forced to conclude that the trochlearis arises *in situ* through the "Umwandlung oder Ausläuferbildung der Ganglienzellen." According to Miss Platt ('91, p. 95), the trochlearis in Acanthias first appears as a small fibrous nerve growing from the constriction between midbrain and hindbrain. This may be followed a short distance into the mesoderm, but, becoming extremely attenuated, is soon lost. "Soon after the appearance of this small nerve, which is the root of the permanent trochlearis,[2] cells are proliferated to meet it from the ganglion cells that lie above the superior oblique muscle. Thus the permanent trochlearis arises from two sources, from the brain and from ganglion cells." Finally, Kupffer ('91) stated that he had found a nerve in Ammocœtes, which he thought to be the trochlearis (for reasons not clear to me), directly connected with the second epibranchial ganglion. Were this opinion correct, the trochlearis would be the serial homologue of a branchial (dorsal), not of a spinal dorsal nerve.

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[1] Confirmed by Oppel, '90.

[2] Miss Platt makes, in my opinion, an unnecessary distinction between a "primary" and a secondary, or "permanent" trochlearis. The "primary trochlearis"

From this summary of previous embryological evidence bearing on the question of the morphology of the trochlear nerve, it is clear that little support is given to the view, based on the later histological structure and relations, that it is morphologically a ventral segmental nerve. Only Kastschenko ('88) finds the nerve in early stages fibrillar in structure. The following evidence, however, leads me to conclude that its mode of development is the same as that of the oculomotorius and abducens, and that therefore it must be regarded, like these, as a ventral (medullary) nerve. I first find the trochlearis in sections of embryos of 19–20 mm. as a fibrillar nerve bundle extending from the dorsal constriction between encephalomeres II and III. Two roots are already present at this stage, but neither in these, nor in the nerve bundle as far as its fibres may be traced in the mesenchymatous tissue at the sides of the brain, are nuclei to be found. While proximally the nerve fibres are united in a compact bundle, they distally separate so as to form a loose brush of structureless fibres, which are lost in the mesenchyma at a considerable distance dorsal to the musc. obliquus superior (Figure K). While I am able to offer no direct evidence in favor of the view that the fibres of the trochlearis, as above described, are processes from neuroblast cells in the ventral horn of encephalomere III, I hold that they are such, since their well known later histological relations support this conclusion. Dorso-ventral fibres in this region of the neural tube may indeed be traced in embryos of this stage, but their connection with the fibres of the trochlearis is not clear to me. The dorsal chiasma of fibres is present.[1] Of a ganglion, or of any grouping of cells which might

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is that portion of the trigeminus Anlage which I have for convenience called its trochlear portion, which persists for some time in the constriction between midbrain and hindbrain vesicles. Since the proof of its morphological value has not been given, and since the "permanent" trochlearis is not developed from the "primary" trochlearis, as Miss Platt herself states (p. 96), the use of the latter term appears to me apt to mislead.

[1] The explanation for this dorsal chiasma may be sought in some physiological advantage in coördination gained, but it may also be seen that in case the dorsal exit of fibres were of physiological advantage, it would be easy for the fibres to

receive the name of ganglion, there is no evidence at this or later stages. The last traces of scattered groups of neural-crest cells found in some (not all) embryos of earlier stages (17 mm.) have been lost.

In embryos of 21 mm. some of the distal fibrils of the nerve appear to have united with migratory cells from the r. ophth. sup. trigeminus, a process in my opinion comparable with that which takes place in the growth of the oculomotorius. At least, in embryos of 21 or 22 mm. the distal portion shows nuclei in relation with the nerve fibres, whereas proximally no nuclei are seen. In still later stages the nerve has a distinctly cellular appearance throughout its length. The nuclei are, however, seen in thin sections to be peripheral in relation to the nerve fibres, as in the oculomotorius (Figure I). The evidence of anastomosis of the fibres of the trochlearis and the r. ophth. sup. trigemini I consider very doubtful. During development the loose brush of fibres at the distal termination of the trochlearis becomes united into a compact nerve stem. It has, therefore, seemed to me that the primary widely spread brush of nerve fibrils may be explained on the ground of advantage gained in seeking the terminal organ, the musc. obliqu. superior.

The phenomena observed by me during the development of the trochlearis are seen to correspond very closely with those observed by Miss Platt ('91). To her, as to me, the trochlearis first appears as a fibrillar process from the dorsal wall of the brain. But while she interprets the evidence of cellular growth toward the advancing end of the nerve as of morphological or phylogenetic significance, I am unwilling to give it such interpretation, since I find that these nuclei have nothing to do with the nerve proper. In my opinion, it is probable that they become converted into the nuclei of Schwann's sheath, an opinion which seems confirmed by their peripheral position in relation to the nerve fibres. When the only sections I possessed were of embryos killed with corrosive-sublimate acetic, and stained with carmine or hæmatoxylin, the evidence seemed to me confirmatory of the view of Froriep ('91), viz. that the trochlearis is differentiated from mesenchymatous cells *in situ.* But better methods of preparation have taught me to distrust that evidence, and the results appeared to me too distinctly contradictory to the later histological

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cross each other in growth, since the direction of their growth would thereby be unchanged. I assume that it is easier for a nerve fibre to grow in a direct line than to bend back and reverse the direction of its growth. The *possibility* even of a primary connection of muscle and nerve appears to me to be excluded in the case of the musc. obliq. sup. and the trochlearis.

structure of the trochlearis to be worthy of trust, or even of serious consideration.

Before closing my account of the development of the cranial nerves and their chief branches in Squalus, I wish to call attention to a phenomenon seen in still later stages of development, already noted by me in a former paper ('97, p. 455). It appears to me a matter of considerable morphological importance that the ganglion of the dorsal nerve of van Wijhe's eighth somite (fourth post-otic) — the ventral root of which forms at this stage the first of the five hypoglossus roots — unites in late stages of development with the ganglion cells near the root of the vagus. Kupffer ('90) was the first to make evident the morphological importance of the clearly marked distinction between dorsal and lateral (epibranchial) ganglia in embryos of Cyclostomata. While in the embryos of Selachii there is not such a clearly marked distinction, there nevertheless exist at the roots of the vagus groupings of ganglion cells, or at least of neural-crest cells (quite distinct from the lateral, epibranchial ganglia of this nerve, the ganglion nodosum), which in my opinion are to be regarded as homologous with the dorsal ganglion of the vagus of Ammocœtes.[1] The evidence of the union of dorsal segmental ganglia in the vagus is as follows. During development the continuous neural crest in the occipital and trunk regions of Squalus becomes differentiated into clearly marked ganglia, lying opposite the myotomes and connected by a cellular "dorsal commissure" (Balfour, '81), as far forward in the embryo as van Wijhe's seventh somite. Opposite the sixth and seventh somites no distinct ganglia appear; but instead a wide sheet of cells, lying in close juxtaposition to the extended roots of the nerve, is observable. While in early stages the ganglion of the eighth somite is separated by a considerable interval from the roots of the vagus, in later stages it approaches these, and in embryos of 30 mm. is seen to be in union with them as a well marked ganglionic appendage. In later stages, its fusion appears complete. The ganglion cells do not degenerate, but send axis-cylinder processes both centripetally and centrifugally, the latter forming the posterior of the *roots* of the vagus nerve. The ganglion of the second hypoglossus root (ninth somite) does not, however, so fuse with the vagus, but is seen in embryos of 50 mm. as a group of cells without nerve relations, so far as I am able to determine, enclosed in the cartilage of the cranium. It apparently disappears in later stages, as does its ventral root, the hypoglossus of the adult having, according to Gegenbaur ('72) and M. Fürbringer (97), only two ventral roots without dorsal ganglia. Since the reduction of dorsal and ventral roots takes place from the anterior towards the posterior, these two ventral roots of the adult hypoglossus are in all probability the posterior of the five roots of the embryo.[1] A similar process of fusion of dorsal ganglia with the dorsal ganglion of the vagus takes place in Petromyzon; but in that animal the fusion of the ganglion — viz. that of the "spinalartige Vagusanhang," which for reasons already stated by me ('97, pp. 454, 455) I regard as the exact homologue of the dorsal ganglion of van Wijhe's eighth somite in Squalus[2] — appears by a comparison of the results of Wiedersheim ('80), Schneider ('80), Ahlborn ('84^a), Hatschek ('92), Kupffer ('96), and M. Fürbringer ('97) to be a variable one. This union of dorsal spinal ganglia with the ganglion of the vagus, taken in connection with the fact previously stated by me ('97, p. 453), that the dorsal ganglia of the glossopharyngeus and vagus lie *primitively*[3] median to the dorsal portion of post-otic somites, is a further link in the chain of evidence which shows that no fundamental distinction between spinal and cranial nerves exists. From the foregoing account it will be seen that, as in the case of spinal nerves, we are able, using as criteria the central and peripheral relationships of the motor fibres, to divide cranial *motor* nerves (roots) into two classes, viz.: (1) dorsal (splanchnic) roots, having their nucleus in the lateral horn of the neural tube and their peripheral distribution in the musculature (ventral) of the visceral arches; and (2) ventral (somatic) roots, which have their nucleus in the ventral horn of the neural tube and their peripheral distribution in the musculature (dorsal) of the somites (somatic musculature). The motor fibres of nerves V, VII, IX, and X belong to the former, and nerves III, IV, and VI to the latter class.

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[1] These are probably the homologues of the intracranial ganglia of Ganoids (see Allis, '97, p. 747).

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[1] Hexanchus and Heptanchus both have *five* hypoglossus roots in the *adult* (M. Fürbringer, '97).

[2] Homologized, however, by Ahlborn ('84^a) with van Wijhe's tenth somite, and by Hatschek ('92) with van Wijhe's seventh somite.

[3] Goronowitsch ('92) first observed in the chick that the topographic relation of the vagus to the head somites is the same as that of the spinal nerves to the trunk somites. Sewertzoff ('95, p. 92) also states that "Die Beziehung der Kopfmyotome zu den Kopfnerven, z. B. zum N. vagus ist dieselbe, wie diejenige zwischen den Rumpfmyotomen und Rückenmarknerven, d. h. sie liegen nach aussen von Nerv (Cyclostomata, Ganoidei chondrostei, Urodela, Reptilia, Aves)." This is stated, however, by Kupffer ('94, '96) not to be a *primitive* relation of the post-otic myotomes in Petromyzon. My own observations and conclusions, however, differ from those of Kupffer (see Neal, '97, p. 453). Miss Platt's ('97) observations on Necturus, and her conclusions likewise, confirm the conclusions of Goronowitsch and Sewertzoff.

While it is possible, as has been stated, to establish a numerical correspondence of encephalomeres and somites, the nerve relations are not so clear. We find, for example, that encephalomeres II, III, and VII are connected by ventral (motor) nerves with somites (van Wijhe's) 1, 2, and 3. Such evidence of a want of segmental correspondence would seem at first sight to render untenable the assumption that encephalomeres have the same segmental value as myelomeres. We have already seen that these two classes of neuromeres have structurally little in common. Moreover, a want of correspondence of encephalomeres and visceral arches is shown by the fact that the *dorsal* motor fibres which are connected with encephalomeres III and V innervate two *successive* visceral arches. In view of this discrepancy in the segmental relations of encephalomeres and nerves, can we regard the former of segmental value? Do they afford evidence in support of the assumption that a Vertebrate head segment is comparable, i. e. homologous, with a trunk segment? Before expressing my own opinion in regard to the answer to this question I will briefly review the interpretations given by previous investigators. Two antithetic views concerning the neuromeres have been given, viz. (1) that they are not of segmental or phylogenetic value, and (2) that they are of phylogenetic value.

VII. Segmental Value of Hindbrain Neuromeres.

a. Non-phylogenetic Interpretation.

In 1877 Mihalkovics, speaking of the foldings in the medulla of birds and mammals, expressed the opinion that the want of correlation between these structures and the nerves and visceral arches seems to favor the view that they are of mechanical origin, i. e. formed by the bending and shoving of the neural tube as it rapidly grows in a confined space. This view seems strengthened by the consideration that the ventral wall of the neural tube of chick embryos is, in early stages, markedly folded into segments, irregular in size and inconstant in appearance, and that these folds in the head region are visibly exaggerated by certain fixing agents which result in shrinking the embryo. Balfour, who with Foster ('74) had been the first to express the opinion that these structures were of phylogenetic significance, afterwards ('81) said that it is uncertain whether they have any morphological significance. In 1892

Froriep, in speaking of neuromeres and their nerve relations, said that these relations are in no way of such a kind that both nerves and neuromeres appear to be constituent parts of a simple organ system. The nerves, especially the trigeminus and facialis, are not so constant in their relation to the folds as would be expected, if the latter were primary segments of the nervous system. It looks much more as if the presence and position of the nerves determines the position of the folds, and as if the appearance of the folds is itself a passive, mechanical one, necessitated by quick growth in length in a confined space. On the basis of his research, he was therefore much inclined to consider these late appearing and transitory segments of the brain as morphologically unimportant phenomena.

Broman ('95) has given a somewhat extended description of the foldings in the hindbrain of a human embryo about three weeks old. Although he nowhere formulates his conclusions as to the significance of the folds, it is evident that he does not regard them as of phylogenetic significance, for he says that the correspondence which earlier investigators have found in their relation to nerves seem to him of little help. In his opinion the results differ too much to allow one to think that a general rule prevails in the Vertebrate series as regards the number and relations of the foldings. The foldings, he says, are intensified in the regions of the greatest flexure of the neural tube, and in these regions the radial arrangements of cells in the foldings is also more marked. This, together with the fact that the foldings are confined to the ventral half of the medulla, harmonizes well with a mechanical explanation of their origin. Upon the evidence that rounded cells (which he thinks are the neuroblasts) with round nuclei may be distinguished in the centre of the most strongly developed parts of the brain foldings, Broman ('95, p. 189) forms an hypothesis concerning the origin of the separation of lateral and ventral roots. He says: "Wenn wir noch einmal alle die oben von mir als Neuromeren bestimmten Falten durchmustern, finden wir, dass nur das als Abducensneuromer bezeichnete die ventrale Wand des Hirnrohres ausbaucht. Alle übrigen sind entweder ganz und gar davon abgedrängt, oder auf dem Wege es zu werden. Dies kann natürlicher Weise ein blosser Zufall bei diesem Embryo sein."

Since Broman's paper is, with the exception of Locy's, the most recent one on the question of neuromeres, I will discuss his evidence and conclusions at some length. It is unfortunate for the purpose of discussion that he has failed to identify correctly the cerebellum Anlage. What he calls Cerebellumanlage is the posterior of the two secondary subdivisions of encephalomere III, as may easily be determined by a comparison of his figures with frontal sections of swine embryos. He says (p. 188), "Die ventrale Ausbuchtung der zweiten Falte kann man also mit vollkommene Sicherheit für die beginnende Ponsanlage, und ihren oberen Theil für die Cerebellumanlage halten." But, as may be determined by the relations of the neuromeres to the ear capsule and to the ganglia of the acustico-facialis and the trigeminus in his figures (Taf. X. Figs. 4, 5), the true Anlage of the cerebellum lies anterior to this and is his "erste Falte," which on theoretical grounds he considers related to the trochlearis nerve. As a result of this mistake it happens that the neuromere which he calls "Abducensneuromer" (VI), and to which on purely theoretical grounds he assigns the sixth nerve, is in reality encephalomere V, which is connected with the acustico-facialis. *With this neuromere the abducens never is connected in any Vertebrate yet studied.* In the swine, as I am able to affirm from my own observations, the abducens arises from the ventral portion of hindbrain neuromere VI, which in the early stages of all Vertebrates lies opposite the ear capsule. In Necturus, the chick, and S. acanthias, its origin is ventral and posterior to the origin of the acustico-facialis. In support of this theory of the mechanical origin of the "Falten," Broman finds that, as a result, as he thinks, of the flexure of the neural tube, those neuromeres which correspond with encephalomeres IV and VI of my figures are wedge-shaped, and that their ventral edges do not reach the ventral wall of the neural tube. Moreover, none of his neuromeres extend to the "Deckplatte." But a study of swine embryos leads me to conclude that this is not characteristic of all mammalian embryos, and indeed that it may be "ein blosser Zufall" in the case of Broman's human embryo. In young swine embryos (killed 19 days after coitus) *none of the neuromeres are wedge-shaped ventrally or dorsally;* moreover, the constrictions between them extend into the Deckplatte. The posterior constriction of encephalomere V extends *across* the Deckplatte until a somewhat later stage, and in this constriction a mass of neural-crest cells persists in a way precisely similar to that in which neural-crest cells in S. acanthias persist in the regions of constriction between the primary brain vesicles (encephalomeres).[1]

From an examination of the evidence presented by those who have held that the neuromeres are purely the result of mechanical influences, it is evident that the chief support for the hypothesis consists, first, in an apparent want of a definite relation of the nerves to the neuromeres in the different Vertebrate groups, — i. e. an apparent inconstancy in the structures themselves, — and, secondly, in the fact that the hypothesis seems to explain the structural conditions presented.

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[1] In connection with this fact, it is to be noted that the walls of the medulla in this region are little distended laterally, which may be ascribed to the influence of the ear capsule. (See Plate 5, Fig. 30.)

I turn now to a consideration of the arguments supporting the view that the neuromeres are of morphological (phylogenetic) importance.

b. Phylogenetic Interpretation.

A phylogenetic interpretation of the foldings of the medulla was first given in 1874 by Foster and Balfour. The following year Dohrn accepted this explanation. Béraneck ('84) showed that in the Lizard the hindbrain folds ("replis") were definitely related to certain nerves. Having later ('87) confirmed his observations by studies of chick embryos, he concluded that the foldings are *the last indisputable remnants of the primitive segmentation of the head.* It is notable that he reached this conclusion notwithstanding the fact that, in his opinion, the segments of the spinal cord do not have the same characters as those found in the foldings of the hindbrain. Subsequent investigators, however, have sought to compare encephalomeres with myelomeres. In 1885 Rabl found in chick embryos a regular folding of the side walls of the myelencephalon, the segments of which showed the same characteristics as the foldings in the region of the spinal cord. During the same year Kupffer ('86), in studies on different Vertebrate embryos, found that the foldings extended into the midbrain region. Because of the relatively late appearance of the folds, — "after the closure of the neural tube, after the formation of three brain vesicles, and long after the segmentation of the mesoderm," — Kupffer thought that there was much against the interpretation of these folds as remnants of a primary general metamerism of the neural tube, but his later observations — previously cited in another connection (p. 174) on an embryo of Salamandra atra at a stage before the closure of the neural plate — led him to believe that in this particular case there is a primary segmentation.

The fact that Kupffer here found eight cross furrows in the brain region, representing as many "ancestral segments," appears to have strongly influenced his subsequent interpretations of the morphology of the forebrain in different Vertebrates, for in his later studies he has sought to find evidence of these eight primary "encephalomeres" in the forebrain and midbrain, *even* "after the closure of the neural tube, and the formation of the three brain vesicles, and long after the segmentation of the mesoderm"!

McClure ('89, p. 435, and '90, p. 37) concluded, from studies on embryos of Amblystoma, Anolis, and chick, "that the symmetrical constrictions or folds found in the lateral walls of the embryonic brain are remains of the primitive segmentation of the neural tube, in part atavistic, extending [from the spinal cord region] into the primary forebrain." The serial homology of the segments of the myelon and the encephalon seemed to him certain, since he found both the structural characteristics and the nerve relations to be the same in the two regions. "The dorsal roots of spinal nerves take their origin from the *apex* of their respective myelomeres in exactly the same manner as the nerves of the medulla do from their respective encephalomeres" ('89, p. 437).

In the same year Miss Platt ('89) also advocated the view that there is a serial homology between the encephalomeres and the segments of the spinal cord. While she agrees with Orr and Béraneck in regard to the number and appearance of the neuromeres and the ultimate relations of the nerves, she finds that the cranial nerves develop from the *constrictions* between neuromeres, precisely as the spinal nerves do. In answer to objections to the attempted homology between cranial and spinal segments, she says that in both head and trunk the segmentation is transitory, and that in both regions it is more manifest in the ventral portion of the neural tube.

The conclusions of Waters ('91) are largely confirmatory of those of McClure, viz. that there is a similar segmentation in brain and spinal cord, with similar sensor nerve relations in both these regions.

Zimmermann ('91), as a result of his studies on rabbit, chick, and Squalus embryos, thinks he is able to confirm Kupffer's discovery of eight primary cephalic segments or "encephalomeres," although his eight "primäre Abschnitte" include forebrain, midbrain, and hindbrain regions, while Kupffer's theoretical conclusion was that his eight "primäre Medullarfalten" do not include the hindbrain.[1] Although Zimmermann states that the spinal cord does not appear segmented, he finds in later stages thirteen homodynamous "encephalomeres," and has given a table of these with their nerve relations. He supposes three roots, a dorsal, a lateral, and a ventral one, to be related to each encephalomere, but his table gives chiefly the impression of numerous gaps to be filled with hypothetical nerve roots.

Herrick ('92) states that he finds the segmentation of the medulla

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[1] At first Kupffer thought they did not include the forebrain!

and spinal cord of snake embryos not explicable on mechanical grounds. "The neuromeres of the medulla cannot be ascribed to the mechanical influence of the Anlagen of the nerves, for those segments which have no nerves develop equally with the others" (cf. Froriep, '91). He considers however "the neuromeres of the forebrain" region wholly illusory from a morphological standpoint, since they involve only dorsal structures.

c. Interpretation of Hindbrain Neuromeres in Squalus acanthias.

I believe that the evidence which I have obtained from a study of the development of hindbrain neuromeres in S. acanthias excludes the possibility of a simple mechanical explanation of them. In their earlier stages they were seen to be local thickenings of the lateral walls, a phenomenon intelligible only on the ground of unequal growth, and not in the least explicable as the result of the passive bending or shoving of a tube already formed.[1] Since the somites do not extend into the region of the dorsal part of the encephalomeres, the possibility that the neural tube in this region is constricted by them is excluded. They are, then, in both structure and mode of development, clearly not to be explained in the same way as the myelomeres. Again, that they are not due to the effect of the Anlagen of the nerves, as supposed by Froriep, is shown by the fact that encephalomere IV develops equally with the others, although there is no nerve in relation with it until a comparatively late stage. Since the fibrillar connection of nerves with neuromeres is established almost at the same time that the inner surface of the hindbrain neuromeres becomes concave, it might be thought that this change is due to the mechanical effect of nerve fibres. That such is not the case seems clear, however, because no nerve fibres come into relation with the outer convexity of encephalomere VI. The hindbrain neuromeres, from their early appearance onwards until they disappear, are local differentations of the walls of the medulla, and as such are not, I believe, to be satisfactorily explained on simple mechanical grounds. On the other hand, I hold that they do possess certain characteristics which admit of a mechanical explanation. This seems to be supported by evidence from two sources. In the first place, a fixing agent which causes a contraction of the tissues of the embryo intensifies the constrictions between the neuromeres. By this means the radial arrangement of cells and nuclei is still more sharply emphasized. I think we may safely assume that this effect is the same as that resulting from a shoving of the neural tube due to rapid growth in a confined space. Figure 28 (Plate **5**) shows a frontal section of a preparation of a shark embryo, nearly 10 mm. long. The specimen was fixed in the mixture of picro-sulphuric and chromic acids, and then transferred directly to 50 per cent alcohol. Inadequate fixation and immediate transference to a fluid of very different osmotic power resulted in a strong contraction of the embryo, particularly emphasized in the wall of the neural tube. (In the figure the constrictions appear exaggerated, since only the regions of the nuclei are shaded.) Moreover, a comparison of embryos of different Vertebrates gives evidence, as it seems to me, that the bending of the neural tube results in the intensification of the characteristics of neuromeres. I have studied in frontal section embryos of Petromyzon, Gadus, Amblystoma, S. acanthias, chick, and swine. The radial arrangement of cells is more pronounced in those forms which have a stronger flexure, and in which, therefore, we may safely assume that there is a greater shoving of the neural tube, due to rapid growth in a confined space. These characteristics are considerably more pronounced in Sauropsida than in S. acanthias, in which the flexure of the neural tube is, however, considerable. This explanation tends to remove the doubt as to the phylogenetic value of such structures as the neuromeres which naturally arises when these are shown to be structures slightly, if at all visible in the lowest Vertebrates (Amphioxus and Cyclostomes), while well marked in the highest. I believe that the presence of yolk makes the conditions in both Petromyzon and Amblystoma less primitive than in Squalus, chick, and swine.

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[1] This is true also in swine and chick embryos; but I do not find in Amblystoma as good evidence that the neuromeres are local thickenings of the neural wall.

In Gadus and Amblystoma the radial arrangement of cells and nuclei is even less pronounced than in S. acanthias, and this seems to be correlated with the fact that the flexure of the neural tube in the former is less marked than in the latter. It must be admitted, however, that the presence of much yolk in the cells of the neural tube of Amblystoma (Plate **5**, Fig. 35), in which no sign of encephalomere IV is present, may be concerned in producing the different condition of this form, in which the outpocketing of the neural tube takes place in the region of the proliferations of the ganglionic Anlagen only. Broman ('95, p. 186) has given proof, satisfactory as it seems to me, that the nuclear and cellular characteristics of the neuromeres of the human embryo may be explained partly on mechanical grounds. Embryologists are agreed that the flexures of the neural tube may be accounted for by the rapid growth of the tube in a confined space. Such growth would clearly result in a shoving of the neural tube, and also in a flexure in weaker portions, as in the regions between local thickenings, like the hindbrain neuromeres. The crowding of the cells in the regions of constriction between neuromeres may be accounted for in the same way. I therefore conclude that *some* of the structural characteristics of neuromeres may be intensified by the bending or shoving of the neural tube during its growth.

The conditions presented in Amblystoma (Plate **5**, Fig. 35) led me to believe at one time that the neuromeres might be related to the proliferation of the cells of the ganglionic Anlage. In this animal the neural tube is evaginated in the regions of the proliferation of cells for the ganglionic Anlagen of nerves V, VII, IX, and X, while in the region where no neural-crest cells are proliferated — the region corresponding to the position of encephalomere IV (in other forms) — no neuromere appears.[1] In S. acanthias we have seen (page 215) that from two of the hindbrain neuromeres, viz. V and VI, are proliferated the cells of two distinct nerve Anlagen. But since no nerve Anlage is proliferated from encephalomere IV, although this is as well marked as other encephalomeres, I was compelled to abandon the hypothesis, to which the study of Amblystoma had inclined me. *The fact that particular nerve Anlagen are proliferated from particular encephalomeres may, however, be a clue to the primitive mutual relationships of these nerves and of the encephalomeres to each other.* The fact that the local thickenings are confined to that region of the neural tube from which the great nerves of the head — V, VI, VII, IX, and X — arise, must also give us some clue as to their significance. Such local thickenings are seen neither in the region anterior, nor in that posterior to the medulla, but they are not limited by the ear capsule posteriorly, and the anterior boundary of them does not coincide with the anterior boundary of the primary hindbrain vesicle. It is to their nerve relations, then, that an investigator must first turn his attention. We have seen that in the development of the neural crest some of the cells of the trigeminus are proliferated from encephalomere III; that few cells are proliferated from encephalomere IV; that from encephalomere V come the cells of the acustico-facialis, from encephalomere VI the cells of the glossopharyngeus, and from encephalomere VII the cells of the Urvagus. The clearly marked relations of the Anlagen of the two suc-

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[1] The migration of cells from certain regions of the neural tube would certainly weaken these regions, and the tube would in consequence, if subjected to a longitudinal pressure, or to distention by growth, tend to bend or distend most readily in such places.

cessive nerves, the facialis and the glossopharyngeus, to two successive encephalomeres (V and VI), seems to me to be a very important fact.[1] The cells of the glossopharyngeus are crowded back by the ear capsule, but the fact that in their ventral course they are directed anteriorly into the third visceral arch goes to prove that their posterior position is not their primitive one. Almost as clear is the relation of the cells proliferated from encephalomere VII to the second branchial (4th visceral) arch. From these facts I was led to think that the primitive relations of the hindbrain neuromeres were with the visceral arches. The fact that the hindbrain neuromeres are local thickenings of the lateral walls of the medulla also leads to the opinion that they are segmental groupings of the "Kerne"[2] of the nerves of the visceral arches. With this hypothesis in mind, I have examined the evidence in S. acanthias, as well as in other forms, in order to see if the facts support it. The more primitive relations would be expected to occur in S. acanthias. From encephalomere III are proliferated neural-crest cells which enter the mandibular arch; later this encephalomere becomes related with the motor root which innervates the muscles of this (mandibular) arch. Its relations, then, are clearly with the first visceral arch, and we may therefore assume that its local thickening contains, at least in part, the "nucleus" of the trigeminus.

The evidence obtained from the study of the relations of encephalomere IV seems at first sight strongly against the hypothesis. Few cells are proliferated from this neuromere. Late in its development the fibres of the sensor root of the trigeminus connect with its convexity. It forms a marked exception in its nerve relations to the other hindbrain neuromeres. Were it not that other facts are found which serve to bring this apparent exception into harmony with the hypothesis, the adverse evidence it presents would seem an insurmountable obstacle to the acceptance of my view. Neural-crest cells which pass into the second visceral (the hyoid) arch are proliferated from hindbrain neuromere V, and the motor fibres in relation with this neuromere innervate the muscles of this arch. From hindbrain neuromere VI are proliferated the neural-crest cells which pass into the third visceral (1st branchial) arch, and the motor fibres of the glossopharyngeus, of which these cells form the ganglionic Anlage, innervate its musculature. The place of origin of the fibres of the glossopharyngeus is crowded backward, evidently by the growth of the ear capsule. The place of origin of the roots of this nerve are variable. In swine and chick, for example, they have their origin from encephalomere VII, while in S. acanthias they arise behind this encephalomere. This is correlated with the fact that the ear capsule in S. acanthias is crowded backward into the region opposite encephalomere VII, whereas in the swine and chick the ear capsule continues to lie opposite encephalomere VI until long after the nerve assumes fibrillar connections with the neural tube. We may thus explain the variation in the position of the roots of this nerve, and still believe from the evidence that their primitive relations were with encephalomere VI.

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[1] Hoffmann ('94) has spoken of the paired segmental outpocketings of the neural tube of this region.

[2] That is, they may be localizations of the motor "Kerne" and of the sensor "Endkerne" of the nerves primitively related to them.

Again, the cells proliferated from encephalomere VII are those which pass into the fourth visceral (2d branchial) arch, and form the Anlage of the Urvagus, whose motor fibres innervate the musculature of that arch. The Urvagus assumes fibrillar connections with the neural tube at a point behind the origin of the glossopharyngeus, and the cause of this change of relation may safely be assumed to be the same as in the case of that nerve. We have good evidence, then, that the primitive relationships of four of the hindbrain neuromeres were with the first four visceral arches. This relationship consists chiefly, but not wholly, in the fact that from these four neuromeres are proliferated cells which enter these arches and there form, in part at least,[1] the ganglionic Anlagen of the nerves related with them. The origin of these cells from the neural crest would naturally lead us to infer that in dealing with them as nerve Anlagen we are not dealing with motor nerves. We are, however, really dealing with the Anlagen of nerves which later become mixed. But in later stages, when the nerve roots are established, the roots of only two of the nerves in question, viz. V and VII, have their exit from the encephalomeres from which their ganglionic Anlagen arose. Have we a right, then, to assume that the exits of the roots of the other two nerves, IX and X (Urvagus), have been pushed back from the position which may be assumed, on the evidence of the relations of their ganglionic Anlagen, to have been the primitive one? I believe that we have, because, as we have seen from the examination of the relations of the roots of these two nerves, these roots lie as close to the point of origin of their ganglionic Anlagen as the ear capsule will permit. In a form like S. acanthias, where the ear capsule shifts backward, the exit of the root of the glossopharyngeus lies behind encephalomere VII, whereas in such forms as the chick and swine, where the ear capsule does not similarly shift backward, the exit of its root is from the expansion of encephalomere VII. In all Vertebrates, the roots of the glossopharyngeus and the Urvagus lie close to each other, but in S. acanthias, where there is a greater amount of posterior displacement than in any other Vertebrate that I have studied, these roots are more crowded together than in other forms. These facts seem to me to warrant the conclusion that the roots of the glossopharyngeus and the Urvagus primitively made their exit from those encephalomeres which give rise to their ganglionic Anlagen. And we may likewise assume that the local thickenings of these encephalomeres have their significance in this primitive relation, i. e. they contained the "Kerne" of these roots. I am able to find no facts which render this assumption untenable.

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[1] Part of the neural-crest cells surrounds the mesoderm of the visceral arches, and very probably gives rise to some of the connective tissue of the arches. (See Plate 6, Fig. 40, *cl. crs. n.*) Whether or not they later form the cartilages of the arches, as they are said to do in Necturus (Platt, '94, '97), is a question which requires more careful and prolonged study than I have been able to give.

On the other hand, encephalomere IV never has nervous connection with a visceral arch. From it few neural-crest cells are proliferated, and in consequence it never forms the ganglionic Anlage of a nerve, nor does it ever in ontogeny have a motor nerve in connection with it. Since the other four encephalomeres are related to visceral arches, I incline to think that this encephalomere was once related to a visceral arch of its own. Otherwise, so far as I can see, its existence is inexplicable. In this condition, then, I find additional evidence of a lost visceral arch, which van Wijhe ('82), Miss Platt ('91^a), and Hoffmann ('94) believe once existed in the region of this neuromere. These investigators have found a want of exact correspondence between the somites and the visceral arches in the region of the spiracular cleft. Van Wijhe was led to believe that the *hyoid* (2d visceral) arch is double, — i. e. represents two arches, the fusion of which has resulted in the obliteration of the visceral cleft between them, — while Miss Platt and Hoffmann have held that the *mandibular* arch is double, and that an anterior gill cleft has disappeared. The disappearance of a visceral cleft is rendered plausible, if we assume that such a loss would greatly strengthen the mandibular arch when it came to function as a lower jaw. The evidence from a study of mesomerism and neuromerism therefore seems mutually confirmatory.

If encephalomere IV was related to a lost visceral arch, it follows that the lost arch must have been situated posterior to the mandibular (1st visceral) arch, for the musculature of this arch is innervated from encephalomere III. It also follows, because of the relation of the nerve of encephalomere V (facialis) to the present spiracular cleft, that this was once the second visceral cleft instead of the first (disregarding for the present the possibility that the mouth represents a pair of gill clefts), as it now is. It seems entirely possible that the outpocketing of the present first visceral (hyo-mandibular) cleft was originally a double one,[1] and that the fusion of these two outpocketings resulted in the loss of the visceral arch which once separated them, and therefore in the loss of the nerve primitively related to that arch. Moreover, between the second head somite of van Wijhe, which extends into the mandibular arch, and the fourth somite, which is widely connected with the mesoderm of the hyoid arch, there lies the third head somite, in correlation with which there is no intermediate visceral arch. This somite (the 3d) lies opposite the posterior constriction of neuromere IV, and speaks plainly for the previous existence of a lost head segment, for which neuromere IV may once have furnished the nerve centre. Did such an arch exist, each of van Wijhe's somites from the second to the sixth, and each of the encephalomeres from III to VII would correspond with a visceral arch.

I give a brief summary of the line of reasoning which leads me to believe that the significance of the hindbrain neuromeres lies in their primitive relationship to the visceral arches. In the young embryos of S. acanthias two facts, both so far as I know new, present themselves. In the first place, the hindbrain neuromeres, five in number, are found to be successive similar thickenings of the lateral zones of the medulla. Secondly, from four of them, viz. III, V, VI, and VII, are proliferated the ganglionic cells of the four cranial nerves which innervate the first four visceral arches, viz. the trigeminus, the facialis, the glossopharyngeus, and the Urvagus. A clue to the significance of the local thickenings of the neural wall in the tract of the encephalomeres is given in the fact that from those two encephalomeres which (in other Vertebrates as well as in S. acanthias) most closely retain these primitive nerve relationships, viz. III and V, emerge the fibres which innervate the visceral arches (primitively) related to them. The thickenings are the first expression of the "Kerne" (nuclei) of the nervous centres related to the visceral arches, and possibly also, primitively, of those related to the somites.

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[1] Kupffer ('93) finds in Acipenser embryos an entodermal outpocketing or pouch, which soon disappears, just anterior to the hyomandibular pouch. The position of this pouch would identify it with the cleft whose former existence seems probable on the evidence given above. Houssay ('91) also recognizes in Amblystoma a visceral cleft between the oral and the hyomandibular.

A study of neural segments anterior and posterior to the medulla has led me to the conclusion that the *local thickening* is a more essential characteristic of a hindbrain neuromere than the commonly accepted criteria, viz. the radial arrangement of cells in the neuromere, and the crowding of them in the regions of constriction between neuromeres, both of which may be the result of mechanical influences.

The shifting of the point of exit of the roots primitively related to encephalomeres VI and VII may easily be explained as the result of the crowding caused by the ear capsule. Since four hindbrain neuromeres are clearly related to four visceral arches, we should expect the remaining one, encephalomere IV, to have been primitively related to a visceral arch. That such an arch has been present in the region of this neuromere during phylogeny, has been made probable by the studies of van Wijhe ('82), Miss Platt ('91), and Hoffmann ('94). The evidences from the study of neuromerism and mesomerism are mutually confirmatory, and to the effect that *a visceral arch has been lost in the region of encephalomere IV and van Wijhe's third somite.* Having established an exact numerical correspondence between encephalomeres and somites (head cavities), and a probable primitive correspondence of hindbrain encephalomeres with visceral arches, I conclude that *in the head region there existed primitively a correspondence between neuromerism, mesomrism, and branchiomerism.* Since this correspondence is not to-day exact in Squalus or in any other known Vertebrate, it seems necessary to discuss somewhat in detail the constituent parts of the anterior or more highly modified metameres, and to inquire what may be inferred as to their previous conditions. The table on the opposite page, although in part theoretical, will help to make the discussion clearer.

I have in this table included neuromeres as far posteriorly as the eleventh. Accepting Hoffmann's ('94) conclusion that vertebral arches as far back as that which corresponds with van Wijhe's tenth somite fuse into the cranium of the adult Squalus,[1] it would follow that neuromeres I to XI would be included in the cranium. The variability in the number of segments added to the occipital region of the cranium in different Selachii and Ichthyopsida (Fürbringer, Sewertzoff) makes the exact number in Squalus a matter of no great morphological importance.

We see that the cephalic segments are highly modified segments altered by reduction or enlargement (possibly even by substitution and change of relation, as, for example, in the case of the vagus segments) of

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[1] Recently confirmed by Sewertzoff ('98).

TABLE III.—NEUROMERES I TO XI IN SQUALUS, AND THEIR RELATIONS TO NERVES, SOMITES, AND VISCERAL ARCHES.

	NEUROMERES	I		II		III		IV		V		VI		VII		VIII		IX		X		XI
CEPHALIC METAMERES.	Somites . . .		a[1]		1		2		3		4		5		6		7		8		9	
	Nerves (dorsal)	I (olf.)		ophth. prof. V		V		(V)[7]		VII		IX		X		X		1st sp.[2]		2d sp.[3]		3d sp.[3]
	Nerves (ventral)		lost		III		IV		(VI)		(VI)		(VI)		VI		1st sp.[4]		1st sp.[4]		1st sp.[4]	
	Visceral clefts			lost		mouth		lost		1		2		3		4		5		6		lost[5]
	Visceral arches		?[6]		?[6]		1		(1)		2		3		4		5		6		lost[5]	

[1] Possibly also representing a visceral pouch.

[2] Fuses with the dorsal ganglion of X in later stages.

[3] Represented by ganglia which probably disappear in development.

[4] Form the first three roots of the embryonic hypoglossus nerve.

[5] Found in Hexanchus, Heptanchus, and Chlamydoselachus.

[6] Possibly represented in the two labial cartilages.

[7] Roman numerals bracketed indicate the theoretical nerve relationships.

parts of the original segments. Fortunately, however, with the knowledge that neuromeres and mesomeres correspond numerically, we are able to see that the majority of changes which have occurred are correlated ones, and therefore capable of explanation. We furthermore see that the greatest changes have taken place in the more anterior metameres, chiefly and primarily by the loss of the ventral parts of these metameres. Since the more posterior of the cephalic segments have indubitable metameric value, I shall discuss in detail only those anterior ones (viz. I to VII) concerning which there is most disagreement among morphologists, beginning with the consideration of the seventh, whose relations are least modified.

VIII. Primitive Relations of Cephalic Segments.

a. Relations of Encephalomere VII.

Opposite the posterior constriction of this encephalomere in very early stages lies van Wijhe's 6th somite, which develops embryonic muscle fibres and is universally considered a true somite. I therefore regard this as the mesomere corresponding with encephalomere VII, whose neural-crest cells first meet the mesoderm opposite the anterior constriction of this somite (Plate **3**, Fig. 13). These cells form the Anlage of the anterior branch of the vagus (Urvagus), and I assume that the primitive relations of this nerve were with the myoseptum between the 5th and 6th somites. The intermediate position of the Urvagus with respect to the myotomes and its ontogenetic union with spinal ganglia in some Vertebrates serves to show that there is no fundamental difference in this respect between cranial and spinal nerves. For reasons which will be stated in connection with the study of the relations of encephalomere IV, I regard the abducens (Plate **4**, Fig. 21), whose fibres have their exit from the ventral horn of encephalomere VII, as representing in part the ventral nerve of this segment. Furthermore, I assume that the mesoderm of the 6th somite was primitively connected with the mesoderm of the 4th visceral arch (Plate **3**, Fig. 16); because that somite in Ammocœtes which I regard as its exact homologue, viz. the 2d post-otic somite, is certainly in early stages thus connected. Consequently the present 3d visceral cleft bounds ventrally the visceral (splanchnic) portion of this segment.

b. RELATIONS OF ENCEPHALOMERE VI.

The present structure and relations of the component parts of what I regard as the primitive sixth cephalic segment have been considerably changed cœnogenetically by the development of the otic capsule. Arising from what in all probability was primitively a sensor organ of the dorsal lateral line (Ayers), the great enlargement and subsequent invagination of this capsule bring about ontogenetically the degeneration of the musculature of the 5th somite, whose cells, after assuming the elongated spindle form of embryonic muscle cells, are transformed in early stages into loose mesenchyma. In Ammocœtes, however, only the median portion of the 1st post-otic somite disappears during ontogeny, while the lateral portion forms the most anterior segment of the lateral body musculature (musc. lateralis capitis anterior, von Kupffer). Furthermore, in Squalus the development of the otic capsule causes a shifting backward of the point of exit of the fibres of the glossopharyngeus, whose ganglion cells were proliferated from encephalomere VI; moreover, the fibres of this nerve may be traced in the neural tube as far forward as encephalomere VI, in which, it is my opinion, their nuclei lie. The growing ganglionic Anlage of this nerve meets the mesoderm between the 4th and 5th somites (Fig. 13), and I assume that it was primitively related, as are the dorsal nerves of Amphioxus, to a myoseptum, i. e. the one primitively between somites 4 and 5. The sensor fibres of this nerve innervate the skin of the present 2d visceral cleft (Fig. 14), which was, I assume, primitively inter-somitic in position and situated ventral to the myoseptum between the 4th and 5th somites. Its motor fibres innervate the splanchnic musculature of the present 3d visceral arch, probably a primitive relation. The abducens nerve, I believe, represents the primitive ventral nerve of this metamere.

c. RELATIONS OF ENCEPHALOMERE V.

The fourth somite, the one corresponding to the fifth cephalic segment, is the most rudimentary of all the cephalic somites. The phylogenetic loss of its musculature and the ontogenetic dissolution of its cells into a loose mesenchyma may be explained as due to the same cause as that operative in the case of the 5th somite, the development of the otic capsule. The dorsal nerve of this segment, the facialis, is inter-somitic in position, occupying the constriction dividing the 3d and 4th somites (Figs. 11–17), and its motor fibres innervate the (splanchnic) musculature of the corresponding (2d visceral or hyoid) arch. Correlated with the loss of the somatic musculature of this segment, a somatic (ventral) nerve is wanting, and as in the case of the 6th segment I assume that this is to-day represented by the abducens. Since the sensor fibres of the facialis innervate the skin of the hyomandibular (1st visceral) cleft, this cleft may be believed to have been primitively situated ventral to the constriction between the 3d and 4th somites. I find no evidence to support the view that the hyoid arch represents two splanchnic segments.

d. Relations of Encephalomere IV.

As has already been stated, there is no ganglionic nerve Anlage proliferated from encephalomere IV, and although the fibres of the major root of the trigeminus have their exit in early stages from its outer convexity, the probability is that such relation of nerve V is secondary, and therefore not of phylogenetic significance. I hold that this encephalomere, by virtue of its local thickening, affords evidence of a lost visceral arch, the loss of which would naturally be correlated with the loss of the dorsal nerve. Since, however, the disappearance of the splanchnic portion of this segment may have been due simply to a union with the corresponding portion of the anterior (mandibular) segment, it is also possible that the dorsal nerve has fused with the nerve of the anterior segment, the trigeminus. This conclusion seems indeed supported by the evidence that at least some of the fibres of the trigeminus roots have their nucleus in the lateral horn of this (4th) encephalomere.

In a scheme of primitive segmental relations such as I am at present advocating, there is likewise difficulty in explaining the fact that the somite (van Wijhe's 3d) which I assume to correspond with encephalomere IV is innervated by the abducens, whose fibres make their exit from encephalomere VII. The evidence which leads me to conclude that the abducens to-day represents the primitive ventral nerve of this encephalomere, as well as those of encephalomeres V, VI, and VII, has been partly given in connection with the study of its development; it may be summarized as follows. (1) Its roots are many (4–6 in various Selachii) and more widely separated than those of any other nerve. (2) Not only do abducens fibres innervate pre-otic musculature (musc. rectus posterior), but fibres from this nerve may also be traced for a considerable distance in the mesoderm of the embryo posterior to encephalomere VII (Fig. 20). (3) The variability as to the place where its fibres emerge, as shown by comparative embryological evidence, appears to indicate that its relations are not limited to any single encephalomere. (4) Its nucleus in the ventral horn of the neural tube is greatly elongated.

(5) In Torpedo it innervates musculature (musc. rectus posterior) derived from *two* somites, viz. van Wijhe's third and *fourth* (Sewertzoff, '98). I am not able, however, to offer direct evidence that the nerve has part of its nucleus in encephalomere IV. I am therefore not able to exclude the possibility that the ventral root of a post-otic somite has been substituted for the pre-otic ventral nerve which once innervated somite 3. That such a substitution of the fibres of a ventral nerve of one segment for those of another may take place ontogenetically, I have the following evidence. I find that in a Squalus embryo of 50 mm. the ventral nerve of van Wijhe's 7th somite has become very rudimentary, while fibres from the ventral nerve of the 8th somite extend to the musculature derived from the 7th somite, which in this stage forms the most anterior segment of the lateral musculature. Now, if the ventral root of the 7th somite atrophies before the adult stage is reached, and if the musculature derived from this somite remains the first segment of the lateral trunk musculature of the adult, as has been stated by van Wijhe ('82) and Hoffmann ('94), the conclusion seems unavoidable that we have to do here with a substitution of a posterior nerve for one farther anterior. Moreover, in Petromyzon we have evidence that the first five post-otic myotomes of the lateral trunk musculature are innervated by the ventral nerves of the last two of the corresponding somites, i. e. the 4th and 5th post-otic, which in my opinion are homologous with the 4th and 5th post-otic somites of Squalus (van Wijhe's 8th and 9th). Here also the conclusion seems to me to be warranted that there has been a phylogenetic, if not an ontogenetic, substitution of the nerves of posterior segments for those of more anterior segments.[1] We may therefore infer, with a considerable degree of probability, that a similar substitution of a post-otic nerve for a pre-otic one may have occurred phylogenetically in the case of the abducens. Such evidence, however, seems to render unwarrantable the assumption of a primary and inseparable connection of motor nerve and muscle. Furthermore, the evidence that the motor nerves develop as axis-cylinder processes of medullary cells given by His ('89) for spinal nerves, and by myself in this

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[1] See Neal ('97, Figure 2, p. 446) for evidence that the fibres of a post-otic ventral nerve (hypoglossus auctorum) extend into the pre-otic region with the muscle they innervate. It would seem a very easy matter for such fibres to come into nervous connection phylogenetically with the eye muscles, and especially the posterior of these, with which in Petromyzon they are very closely connected. Hatschek ('92) stated that the musc. rectus posterior becomes connected with the anterior of the post-otic myotomes. See evidence given by M. Fürbringer ('97) and Neal ('97) upon this question.

paper for cranial ventral nerves in Selachii, leads to the same conclusion. The visceral cleft which defined anteriorly the splanchnic part of the fourth segment is not ontogenetically evident in Squalus. Kupffer ('93) has possibly seen evidence of a rudimentary cleft between the mouth and the hyomandibular cleft of Acipenser. And possibly this cleft may be represented in the "Pseudobranchialrinne" of Amphioxus.

e. Relations of Encephalomere III.

As in the case of the four posterior hindbrain segments, the study of the development of the nerves connected with encephalomere III (Hinterhirn) gives the clue to the primitive relations of this primary vesicle. The neural-crest cells proliferated from it pass ventrally into the mandibular arch. From a part of these a large ganglion is formed (the Gasserian), through which pass the motor fibres, whose nucleus is, at least in part, in encephalomere III, to innervate the musculature of the first visceral (mandibular) arch. We have thus the splanchnic elements of a cranial segment. In the Table of Nerve Relations (p. 253) the trochlearis has been given as the ventral (somatic) nerve of this segment. The evidence in favor of this view has already been stated, and consists in the facts that it innervates musculature derived from dorsal (somatic) mesoderm, that its fibres develop as processes of neuroblasts in the neural tube, and that its histological relations and structure in the adult show it to be a purely motor nerve with motor nucleus in the ventral horn of encephalomere III. I regard the mouth as representing the fused visceral clefts which bounded anteriorly the splanchnic portion of this segment. We have thus all the essential elements of a head metamere.

f. Relations of Encephalomere II.

From the simple dorsal expansion of encephalomere II are proliferated cells which pass ventrally and fuse with the skin to form the mesocephalic ganglion[1] lateral to the 1st somite (Figs. 17 to 20). Although this ganglion never becomes connected with the midbrain (encephalomere II), since its fibres enter the brain through the r. ophthalmicus profundus V, it must in my opinion be regarded as a segmental ganglion comparable with those of the following cranial nerves; the ophthalmicus profundus must likewise be considered as a dorsal nerve homodynamic with the succeeding cranial nerves. Its want of motor fibres may be explained as resulting from phylogenetic loss, since in

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[1] This ganglion is homologous with the first trigeminus ganglion of Cyclostomes.

Myxinoids this nerve possesses motor fibres (J. Müller, P. Fürbringer, Price), and its segmental value as a dorsal nerve seems thereby established. The fact that the fibres of the ophth. profundus V enter the brain at a point posterior to encephalomere III, instead of anterior to it, as they should in order to conform to my scheme of segmental relations, appears to me no serious objection. That they enter the brain at a point posterior to that at which the motor fibres innervating the mandibular musculature enter, and in consequence cross these fibres in the mesocephalic ganglion, is to be explained by the tendency, especially of the sensor cranial nerves, to enter the brain as near the otic capsule as possible (see Ahlborn, '84^a), and by the more conservative relations of the motor fibres (roots) generally.

In my preliminary paper I placed tentatively the so called "thalamic" nerve as the possible dorsal nerve of encephalomere II. Now, however, I question the correctness of this opinion. We certainly need something more than a strand of neural-crest cells which persist for some time in a region of constriction between encephalomeres, but *which never assume fibrillar relation with the neural tube*, to warrant us in assuming that we have to do with a *nerve.*[1]

The development and relations of van Wijhe's first somite and of the oculomotorius leave no doubt that in them we have the somatic elements of a metamere. Probably no ventral or splanchnic portion of the mesoderm of this segment exists, consequently the r. ophthalmicus profundus possesses no splanchnic fibres.[2] In my opinion it is doubtful if the hypophysis may be regarded as evidence of an ancestral visceral cleft between segments I and II.

However, I hold that the structural comparability of encephalomere II with hindbrain encephalomeres, together with the evidence of its relation with a segmental ganglion, and of its connection with somatic musculature by means of a ventral motor nerve, strongly favors the view that it is serially homologous with hindbrain encephalomeres.

g. Relations of Encelphalomere I.

, That which I regard as the first cephalic segment of Craniota consists of an encephalomere (primary forebrain) which has been shown to be

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[1] Kupffer excels Miss Platt in discovering "rudimentary" nerves, but until we have a better criterion for a nerve than a cellular strand there is no reason why the number of "rudimentary" nerves should not be much larger than it is at present recognized to be.

[2] Possibly the skeletogenous element of the ventral portion of this segment is to be found in the "maxillar Lippenknorpel" of Gegenbaur.

morphologically comparable with the hindbrain encephalomeres. It is in connection with a sensor nerve, the olfactory, which appears comparable with the sensor portion of a dorsal segmental nerve in so far as it is composed of bipolar ganglion cells which send their fibres into the brain and, in my opinion, are in part derived from the neural crest. My observations upon this point, however, are as yet incomplete. The want of motor fibres in the dorsal nerve of this segment is correlated with the want of splanchnic musculature.[1] That structure which I, in agreement with Miss Platt ('91) and Hoffmann ('94 and '96), regard as a rudimentary somite (compare Plate **3**, Figs. 16, 17, *cav. a.*), — since it resembles the following somites and gives evidence of producing rudimentary muscle cells, — represents the somatic portion of this segment. In correlation with the want of fully developed musculature, no ventral somatic nerve is present. Van Wijhe ('86^a, p. 680) wrote: "Wenn der Olfactorius ein segmentaler Nerv wäre, müsste man bei demselben das ursprüngliche Vorhandensein eines Somiten und einer zugehörigen ventralen Nervenwurzel annehmen. Von beiden ist keine Spur vorhanden." So far as the somite is concerned, it appears that in the "anterior somite"[2] we now have the requisite evidence. The lateness of the differentiation of the "premaxillar Lippenknorpel" makes it seem at most only remotely possible that it may be regarded as the ventral skeletogenous element of this segment.

h. Comparison with the Segmentation of Amphioxus.

A comparison of the segmentation of Squalus as shown in Table III. (p. 253) with that of Amphioxus is of interest, inasmuch as it appears to favor important conclusions reached by the study of Squalus alone. However, before stating my own conclusions concerning the primitive metamerism of Amphioxus and the homologies of its segments with those of Squalus, it will be well to review the conclusions of previous investigators.

A comparison of their results may be made in the form of a table on the opposite page (after M. Fürbringer, '97, p. 643, slightly modified).

While Hatschek ('92), Willey ('94), and M. Fürbringer ('97) homologize the mouth of Amphioxus with that of Tunicates and Craniota, but

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[1] Likewise in Amphioxus the anterior dorsal nerve is generally believed to be purely sensor in function.

[2] Van Wijhe ('82) saw the "anterior somite" in Galeus, but unfortunately possessed only one embryo; he was therefore unable to express an opinion concerning its segmental value, based on a knowledge of its development and differentiation.

TABLE IV.

	FATE OF		HATSCHEK, '92.	VAN WIJHE, '93.	WILLEY, '94.
1	Unpaired mouth.		Single persisting mouth, the homologue of the median unpaired mouth of Tunicates and higher Vertebrates.	Primary mouth (Autostoma) pushed toward the left and modified to form the pre-oral pit (Räderorgan).	Single persisting mouth, the homologue of the mouth of Tunicates and higher Vertebrates.
2	1st visceral pouch (vorderes Entodermsäckchen) of Hatschek.	Right.		Perhaps the homologue of the 1st head cavities (1st somites) of Selachii.	Probable homologue of the right 1st (premandibular) head cavity of Craniota.
		Left.	Pre-oral pit (Räderorgan; Sinnesorgan).	Pre-oral pit; also primary mouth (Autostoma).	Pre-oral pit, probable homologue of the left 1st (premandibular) head cavity of Craniota.
3	2d visceral pouch of Hatschek (1st visceral cleft of van Wijhe and Willey).	Right.	Right pseudo-branchial groove.	Club-shaped gland.	Club-shaped gland.
		Left.	Left pseudo-branchial groove.	Secondary permanent mouth (Tremostoma). (Spiracular cleft of Selachii.)	1st (abortive) primary gill slit.
4	3d visceral pouch of Hatschek (2d visceral cleft of van Wijhe and Willey).	Right.	1st permanent right visceral cleft.	Lost.	2d (1st permanent) secondary or right gill slit.
		Left.	1st permanent left visceral cleft.	Lost.	2d (1st permanent) primary gill slit.
5	4th visceral cleft of Hatschek (3d visceral cleft of van Wijhe and Willey).	Right.	2d permanent right visceral cleft.	1st permanent right visceral cleft.	3d (2d permanent) right gill slit.
		Left.	2d permanent left visceral cleft.	1st permanent left visceral cleft.	3d (2d permanent) primary gill slit.

deny its gill-cleft nature (Dohrn), van Wijhe regards it as a visceral cleft on the left side, antimeric to the club-shaped gland, which with Willey he regards as a modified visceral cleft, exactly homologous with the hyomandibular (spiracular) cleft of Craniota. Van Wijhe ('93, p. 155) finds evidence of a primary unpaired mouth in the external opening of the left anterior entodermic diverticulum known as the preoral pit (Räderorgan). Homologizing the "Gehirnanschwellung" of Amphioxus with the "Gehirnblase" of the larvæ of Ascidians, he considers it impossible to homologize the mouth (tremostoma) of Amphioxus with the median dorsal mouth of Tunicates, since in the former the mouth and its antimere are laid down immediately *posterior* to the brain vesicle, whereas in the latter the mouth arises in the median plane immediately *anterior* to the brain vesicle; however, the *visceral clefts* of the young Ascidian larva are laid down, like the mouth of Amphioxus, immediately behind the brain vesicle. Moreover, van Wijhe holds that the mouth of Amphioxus is an organ of the left side only, and on the following grounds (quoted from Willey, '94, p. 178): "The outer muscle of the oral hood represents the anterior continuation of the *left half only* of the transverse and subatrial muscles. The inner nerve-plexus of the oral hood is formed on both sides exclusively from nerves which arise from the left side of the central nervous system. The velum is innervated entirely from nerves of the left side," viz. branches from the 4th, 5th, and 6th left dorsal nerves.

Willey ('94) finds evidence to support his view, that the mouth of Amphioxus represents the median dorsal mouth of Ascidians, in the marked asymmetrical conditions of the larva, for which van Wijhe's observations and conclusions afford no explanation. Affirming the asymmetry to be non-adaptive and non-advantageous (*contra* Korschelt und Heider), he concludes that it is the mechanical result of the (phylogenetic) forward extension of the notochord, an extension which is advantageous to an animal which bores in the sand. Hatschek ('92) and M. Fürbringer ('97) agree with Willey in this explanation as to the homology of the mouth of Amphioxus, but bring forward no evidence to support their view. There is no disagreement in homologizing the anterior entodermic diverticula (vordere Entodermsäckchen) of Amphioxus with at least part of the premandibular head cavities (1st somite of van Wijhe) in Craniota.

From the foregoing review it will be seen that two very important questions concerning the nature and homologies of the Vertebrate mouth remain in dispute, viz.: — 1. Is or is not the mouth of Amphioxus to be homologized with the mouth of Ascidians? 2. Is it or is it not homologous, either wholly or in part, with the mouth of Craniota? Upon the answer to the former question would seem to depend the settlement of the question whether the mouth of Amphioxus may or may not be regarded as a visceral cleft, for there is no reason to believe that the mouth of Ascidians represents a pair of visceral clefts. Notwithstanding that Willey appears to have in the asymmetrical mouth of Amphioxus strong evidence in favor of his homology, which has also met the approbation of Marshall ('93), I consider the different relation of the Tunicate and Vertebrate mouth to the brain vesicle a very serious objection to his theory. Furthermore, the presence of a preoral intestine in Vertebrates, which in Squalus extends (morphologically) anterior to the infundibulum, — even to the neuropore, as does the intestine of Tunicates, — leads me to agree with Beard, Kupffer ('88 and '91), and van Wijhe ('94), that in the present mouth of Vertebrates we have a *neostoma*, and also that a *palæostoma* homologous with that of Tunicates must be sought in an anterior opening of the preoral intestine. Kupffer finds evidence of this *palæostoma* in the ectodermic invagination of the hypophysis towards the "Preoraldarm," while van Wijhe finds it in Amphioxus, as stated in the Table, in the actual opening of the preoral intestinal diverticulum of the left side as the preoral pit (Räderorgan).

Waiving the question as to which, if either, of these theories is correct, I regard the mouth of Ascidians as opening at the morphologically anterior end of the alimentary canal; for there appears to me nothing in the literature upon Tunicates to show the presence of a preoral intestine in these forms. The mouth of Appendicularia, which has no "preoral lobe," (though homologized by Willey with the preoral intestinal diverticula of Amphioxus and the premandibular cavities of Craniota,) has a terminal position.[1] According to Willey the method of formation of the preoral lobe in those Ascidians possessing such is as follows (p. 218): "When the larva first hatches, the entoderm and ectoderm are in contact with one another at the anterior extremity of the body, just as they are in the earlier stages. Soon, however, the ectoderm, with the adhering papillæ, springs away from the endoderm at this point, leaving a space into which the two lateral mesodermic bands force their way. In this way a special anterior portion of the body cavity, præoral and præenteric, is produced, and is at first completely filled by a compact mass of rounded cells derived from the mesodermic bands. . . . The anterior, or præoral portion of the body cavity, of which we have just traced the origin, is, and subsequently becomes in a still more pronounced way, the *cavity of the snout*, or *præoral lobe*."

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[1] Willey ('94, p. 277) writes: "Whatever the truth may be as to the precise systematic position and phylogenetic value of Appendicularia, one thing, to my mind, remains absolutely certain, namely, that it has descended from a form which possessed a præoral lobe, and that it has secondarily lost that structure."

On the other hand, the preoral "head cavities" of Amphioxus, which Willey homologizes with the "preoral lobe" of Ascidian larvæ, are formed, as stated by Hatschek ('81), from an abstricted portion of the preoral archenteron. The differences in the formation of these two structures, therefore, seem too striking to permit their being considered completely homologous with each other.

Evidence has already been given in this paper which, in my opinion, makes it impossible to homologize the preoral "head cavities" (anterior entodermic diverticula) of Amphioxus with the "premandibular head cavities" of Craniota. The morphologically anterior portion of the archenteron, the "anterior head cavities" (Platt), are the only structures in higher Vertebrates which, in my opinion, can be homologized with the "head cavities" of Amphioxus. Homologizing, therefore, the "anterior head cavities" in these two forms, I submit on the opposite page for comparison with Squalus the table of the anterior eleven segments in Amphioxus as I interpret them.

If we compare Tables III. (p. 253) and V., we find the following fundamental resemblances in the segments of Squalus and Amphioxus.

Of the component elements of the *first segment*, that which I have regarded as the somatic element, consists of paired cavities cut off from the anterior portion of the archenteron. Since in both cases these cavities represent ventral as well as dorsal and lateral portions of the archenteron, it is impossible to contend that they contain only the mesodermic element of the segment. It seems not improbable that potentially they represent also the visceral-pouch element between this and the following segment. The opening of the left of these in Amphioxus to the exterior as the preoral pit may be regarded as evidence favoring this view. Moreover, M. Fürbringer ('97, p. 633) finds a late differentiated and rudimentary myotome, which lies anterior to the dorsal paired nerves II, which would, if present as stated by him, represent the mesodermic element of this segment, and the "anterior head cavities" would in consequence necessarily be regarded as modified or abortive visceral pouches, as held by Kupffer. Since my sections of Amphioxus give me no evidence of this rudimentary myotome, I hold

TABLE V.—METAMERISM OF AMPHIOXUS.

SEGMENTS	I		II		III		IV		V		VI		VII		VIII		IX		X		XI		XII	
Somites		a[1]		1		2		3		4		5		6		7		8		9		10		11
Dorsal nerves	I		II		III		IV		V		VI		VII		VIII		IX		X		XI		XII	
Ventral nerves		lost		1		2		3		4		5		6		7		8		9		10		11
Visceral clefts (r.)			lost		c.s.g.[2]		lost		1*		2*		3*		4*		5*		6*		7*		8*	
" " (l.)			lost		M.[3]		1		2*		3*		4*		5*		6*		7*		8*		9*	

[1] Possibly representing also a visceral-pouch element.

[2] Club-shaped gland.

[3] M. Mouth.

The permanent visceral clefts are indicated by asterisks.

with van Wijhe, Hatschek, and Willey, that the first myotome in Amphioxus is situated behind the first two pairs of nerves, and also that the "anterior head cavities" of Amphioxus represent the somatic elements of the anterior segment in Craniota. From this point of view, the different fates which the two cavities in Amphioxus undergo, as well as the loss of musculature, is to be regarded as cœnogenetic. The dorsal nerves in both forms are exclusively sensor in correlation with the loss of splanchnic musculature.[1] The unpaired olfactory of Amphioxus is to be compared with the long persisting median connection of the neural tube and olfactory plate in Squalus (*lobus olfactorius impar*, Kupffer). No somatic musculature and no ventral nerves are developed. I regard the cerebral vesicle of Amphioxus, since it is limited posteriorly by the tuberculum posterius (Kupffer), as homologous with the primary fore-brain of Squalus, and therefore as the neuromeric element of the first segment.[2] Whether or not the visceral cleft of this segment is represented in the "anterior entodermic diverticula" (anterior head cavities), I am not able to assert with any degree of positiveness. Fürbringer's discovery appears to favor this view.

In the *second segment* a well developed myotome and ventral nerve develop. In both forms the dorsal nerve of this segment appears to be exclusively sensor. In Myxinoids, however, the dorsal nerve (ophthalmicus profundus) has motor fibres, and it appears to me not improbable that such will be found in its homologue in Amphioxus.[3] If the visceral-cleft element in this segment is not represented in the "anterior head cavities," this may be assumed to have disappeared phylogenetically. All the components of the *third segment* are present, viz. somatic and splanchnic musculature, dorsal and ventral nerves, and visceral clefts.

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[1] The homology of the olfactorius (I) with the first paired nerve of Amphioxus has already been asserted by Owen (1866). The first paired nerve of Amphioxus according to Owsjannikow (1866) and Rabl ('89) is homologous with trigeminus; with r. orbito nasalis or r. I. trigemini (Huxley, 1874); with opticus (Schneider, '79); with part of trigeminus (Rohon, 1881, and Krause, 1888); with ophth. prof. trig. (Hatschek, '92); and with nervus apicis (van Wijhe, '93).

[2] Kupffer ('93) homologizes the cerebral vesicle of Amphioxus with the Vorhirn (Vorderhirn and Mittelhirn) of Craniota.

[3] The second paired nerve of Amphioxus has previously been homologized with part of trigeminus by J. Müller (1842), W. Müller (1875), and Krause (1888); with trigeminus by Goodsir (1841); with trigeminus and vagus by Quatrefages (1845) and Owen (1866); with facialis by Owsjannikow (1867); with opticus by Hasse (1876); with part of trigeminus and with facialis by Rohon (1881); with acustico-facialis by Rabl ('89); with trigeminus exclusive of ophth. profundus by Hatschek ('92); and with ophth. profundus by van Wijhe ('93).

I regard the mouth of Amphioxus as homologous with the left half of the mouth of Craniota and the club-shaped gland as its antimere. That the mouth of Amphioxus as an organ of the left side is exactly homologous with the left half of the mouth of Squalus appears to me probable on the *a priori* ground that it is improbable that an organ of the same function should be twice acquired in the Vertebrate series; and also because the region of fusion of endoderm and ectoderm to form the mouth cleft is in both these forms ventral to the constrictions which separate the second and third mesodermic segments (1st and 2d myotomes). The club-shaped gland also appears as an entodermic diverticulum below the constriction between the second and third mesodermic segments of the right side, that is, opposite the mouth diverticulum, and I therefore, in agreement with van Wijhe ('93), regard it as the antimeric gill cleft.[1]

In the *fourth segment* the following points of resemblance are to be noted. Somatic musculature and a somatic ventral nerve are present. While in Squalus the pair of visceral clefts which bounded anteriorly the splanchnic portion of this segment have disappeared, leaving no trace behind except in the neuromere with which they were connected, in Amphioxus only the right visceral cleft has been thus lost. The left visceral cleft, however, disappears ontogenetically without leaving a trace behind it. A further difference in the two forms appears in the fact that, whereas in Squalus the dorsal nerve has disappeared (or fused with the trigeminus), the dorsal nerve of the left side in Amphioxus is the first of the nerves which innervate the musculature of the velum (van Wijhe).

With the *fifth segment* in both forms begin the permanent visceral clefts. In agreement with Willey ('94), I regard the first secondary cleft as antimeric to the second primary cleft. Their fusion with the ectoderm below the mesodermic constriction between mesoderm segments 4 and 5 (myotomes 3 and 4) is the evidence for their relation to this, the fifth segment. I therefore consider *the first pair of permanent visceral clefts in Amphioxus as the exact homologues of the hyomandibular clefts of higher Vertebrates.* As has already been stated by Willey ('94), all except eight of the primary clefts (starred in the table), which become paired with eight antimeric clefts, undergo atrophy. In conse-

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[1] Willey ('94) gives reasons for regarding the club-shaped gland as the antimere of the first primary visceral cleft. His reasons are based on topographic relations in stages when the primitive topographic relations are considerably changed, and they seem to me less strong than the reasons stated by van Wijhe and myself.

quence there is found at the end of the larval period a "critical stage" of considerable duration, when *Amphioxus possesses eight visceral clefts, which*, if the homology above be correct, *are exactly homologous with the eight morphological clefts of Heptanchus* (*Selachian*) *and Petromyzon* (*Cyclostome*). The evidence of the exact homology of the mouth and visceral clefts of Amphioxus at its critical period with those of Craniota appears to me strongly confirmatory of the truth of the exact homology of segments in Amphioxus and Squalus as stated above.

i. General Conclusions.

The exact numerical correspondence of neuromeres (encephalomeres) and somites has been found not to be a purely accidental one. The ventral motor nerves (oculomotorius and trochlearis) of two successive encephalomeres, viz. II and III, are connected with two successive somites, viz. van Wijhe's 1st and 2d, and the nerves VII, IX, and X (Urvagus), by their topographic relations to successive somites 4, 5, and 6, show a similar metameric correspondence between encephalomeres and somites. Where correspondence does not clearly exist to-day, as in the case of the abducens nerve, we have developmental evidence which suggests how such modifications may have taken place.

Thirteen years ago Ahlborn ('84^a), as a result of his examination of the evidence presented by van Wijhe ('82), stated it as his conclusion that in the head we have a dysmetameric neuromerism, which no longer repeats the metamerism of the mesomeres (somites), but is related to a series of other conditions dependent on both ectoderm and entoderm. Ahlborn likewise concluded that branchiomerism and mesomerism do not correspond. "Gegenbaur's assumption, that the segmentation of the cranial nerves, related as they are to visceral arches, is comparable to the segmentation of the spinal nerves, which correspond with somites, still remains to be proved." The evidence presented above certainly tends to make the assumed correspondence of mesomerism and branchiomerism more probable, and thus indirectly to prove the homodynamy of the nerves which innervate mesomeres and branchiomeres. The recent evidence presented by Hatschek ('92), Kupffer ('91, '96), Price ('96), and Miss Platt ('97) from their studies on Amphioxus, Cyclostomes, and Amphibia points in the same direction, and thus favors Gegenbaur's assumption. The comparative embryological evidence which has been given shows, however, that the adoption of Gegenbaur's view by no means necessitates the assumptions later made by him ('87), viz.: (1) that the head primitively ended with van Wijhe's 6th somite;[1] (2) that between this and the following somite segments (dorsal as well as ventral) have been phylogenetically lost; and (3) that the head primitively ended with the gill region. It has been shown, I believe, that the probable phylogenetic and actual ontogenetic disappearance of visceral clefts does not necessitate the loss of the corresponding mesomere and neuromere. It is true that we have very good reason to infer a phylogenetic loss of distinctly differentiated somites and neuromeres in the Vertebrate series. It is also true that we find evidence of an ontogenetic disappearance of mesomeres. Nevertheless such evidence does not prove that somites have been phylogenetically lost from the occipital region before the group of Selachii, of which Squalus is one of the most primitive forms, is reached. I believe that the evidence which has been given of the complete metameric correspondence of neuromeres and mesomeres — that the Selachian embryo is in this respect an unbroken continuum — renders it unnecessary to assume that somites have been so completely lost that no traces of them appear phylogenetically in Selachii. It is no longer necessary to assume a palingenetic portion of the Vertebrate head which ended with the sixth visceral arch of Selachii (Gegenbaur), or an exact homology between the hypoglossus roots (surely a most uncertain "fixed point") of adult Vertebrates (M. Fürbringer). The evidence which I have given seems thus to favor the opinion of Sewertzoff ('95), that we have "keinen Grund, vorauszusetzen, dass zwischen den palingenetischen Somiten v. Wijhe's (I–VI) und den coenogenetischen (VII–IX) ein Wegfallen der Segmente stattgefunden hat. Wir sehen sine vollkommen regelmässige Anlage der Kopfsomiten und ein eben so regelmässiges [ontogenetic] Verschwinden derselben."

I am aware, however, that the structural differences between the hindbrain neuromeres, e. g. IV to VII, and the neuromeres immediately

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[1] The suggestion that the gill region is not confined to the head region was first made by Huxley ('58). I believe that direct evidence in favor of this suggestion is furnished by Amphioxus (Hatschek, '92), and by Myxinoids (Price, '96). In this connection, moreover, it is of interest that in my previously ('97) made homology the *last* visceral cleft in Ammocœtes primitively bounds *posteriorly* the segment which is homologous with the *last* cranial segment (Hoffmann, '94) of Squalus, viz. van Wijhe's 10th somite. Furthermore it has been shown (p. 268) that this last visceral cleft of Petromyzon is exactly homologous with the last visceral cleft of Amphioxus in its "critical stage" of development. It should, however, be noted that there have been published three other interpretations of homologies between Selachii and Cyclostomata, differing from that made by me, viz. those by Ahlborn ('84^a), by Hatschek ('92), and by Sewertzoff ('95).

following these may seem to favor Gegenbaur's view that the former belong to a palingenetic portion of the Vertebrate head which ended with the 6th (van Wijhe's) somite (bounding neuromere VII posteriorly and ventrally). The structural gap between the seventh and eighth neuromeres is not, however, so sharp that it should outweigh evidences of similarity, and especially the evidence that somites 6 and 7 are indisputably serially homologous. I must confess that I cannot see that the assumption of palingenetic and cœnogenetic portions of the Vertebrate head has added to the clearness of our morphological conceptions, nor can I see that it is rendered necessary by any ontogenetic or phylogenetic evidence now in our possession. Note, furthermore, the disagreement of opinion as regards what is and what is not *palingenetic* or cœnogenetic among those who have been prominent as advocates of this view, viz. Gegenbaur ('87), his pupil, Fürbringer ('97), and Miss Platt ('97). While Gegenbaur holds that van Wijhe's 6th somite is palingenetic, Fürbringer regards the 6th, and possibly the 5th and 4th somites, as *cœnogenetic*. Miss Platt, on the other hand, believes that the 4th and 5th somites are palingenetic, but that the 6th somite is probably cœnogenetic. All this appears to me confusing and unnecessary. The terms cœnogenetic and palingenetic are purely relative terms. I hold the view that each metamere of the head may be regarded as cœnogenetic in comparison with the metameres anterior to it, the head gradually receiving accessions from the trunk. Gegenbaur's famous "Kritik" of 1887 appears more an attempt to establish the visceral arches as the *essential* criteria of cephalic metameres, than a wholly unprejudiced effort to weigh the evidence both anatomical and embryological which was at his command. I believe that the evidence given in the present paper tends to strengthen the generally accepted opinion, which Gegenbaur has sought to overthrow, that the mesomeres in the head, like those in the trunk, afford the most trustworthy criteria of metamerism. The dorsal (neuromeric and mesomeric) segmentation must be regarded as more conservative than the ventral (branchiomeric or splanchnic) segmentation. The lost elements are chiefly the ventral ones. Their loss has indirectly caused the losses in the dorsal elements, such as the disappearance of splanchnic motor fibres from dorsal nerves and (?) of the thickening of the lateral zones of encephalomeres I and II.

It appears to me that the evidence now in our possession gives reason to hope for an eventual solution of the head problem, not only as regards the nature, but also the number of head segments. The problem, it is true, is easier for occipital than for pre-occipital segments. The serial homology of occipital with trunk segments is not generally questioned at present. A comparison of the integral parts of occipital and trunk metameres shows that the belief in their serial homology is well founded. It must, however, be admitted that occipital metameres show no evidence of either excretory or reproductive organs. Nevertheless we may readily believe from the evidence of these organs in the gill region of Amphioxus that this is a cœnogenetic loss in the Vertebrate series. The chief grounds for belief in the homology of trunk and occipital metameres are these: (1) Occipital somites with their (2) ventral nerves are undoubtedly the serial homologues of trunk somites with their ventral nerves. This evidence alone has convinced most morphologists. But there are still other reasons. With our present knowledge, we may, I think, affirm that (3) dorsal occipital (or cranial) and dorsal spinal nerves are serial homologues. One by one, since the discovery by Schneider ('79) of ventral nerves in Amphioxus, the differences between dorsal spinal and cranial nerves, which were at one time or another maintained, have been with increased comparative embryological and anatomical knowledge shown to be unessential. The evidence given by Schneider ('79), Hatschek ('92), and van Wijhe ('93) shows that dorsal nerves, as seen in Amphioxus, are mixed in function, innervating the skin and splanchnic musculature, while ventral nerves are motor in function, innervating somatic musculature. The typical cranial nerves of Craniota, viz. V, VII, IX, and X, are morphologically comparable with the dorsal nerves of Amphioxus, and are therefore to be regarded, as Balfour for other reasons regarded them, more primitive than the *spinal* nerves, which lack the lateral and dorsal (except in Cyclostomes) cutaneous branches.[1] The recent researches of von Lenhossék ('90), Ramon y Cajal, and Kölliker, by demonstrating the existence of non-ganglionic fibres in the dorsal spinal nerves of Craniota, which by their relations must be regarded as motor in function, have shown that in this respect spinal nerves do not differ from cranial. Moreover, in view of the evidence given by Goronowitsch ('92), Sewertzoff ('95), Neal ('97), and Miss Platt ('97), it can no longer be

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[1] The place of these branches has been usurped by the lateral branches of the vagus, as I believe has been suggested by Eisig. The advantage in greater centralization is obvious. If it be true, and it is generally admitted, that cranial nerves receive cells from the skin while the spinal nerves do not, an explanation of this also is seen in the extension of the vagus and the concomitant loss to spinal nerves.

truthfully said that cranial nerves differ from spinal in that the former extend laterad and the latter mediad of the mesomeres. We must conclude that dorsal nerves were in all probability, as in Amphioxus, related to the septa between myotomes. Finally, the distinction made by His, in the case of dorsal cranial nerves, between dorsal (sensor) and lateral (motor) *roots*, has, with the knowledge of the facts above stated, an anatomical and physiological rather than a morphological interest. I therefore see no escape from the conclusion that the occipital region of the head is not a region *sui generis*, and I pass to the consideration of the pre-occipital segments.

To those who are deeply impressed with the differences between post-otic and pre-otic regions of the Vertebrate head, it is necessary to emphasize the following fundamental resemblances in the segments of these two regions. (1) Pre-otic and post-otic encephalomeres have been shown to be morphologically comparable. (2) The dorsal nerves connected with these, and (3) the visceral arches which these nerves supply are in these two regions serially homologous. Moreover, as evidence pointing in the same direction, it may be stated that (4) a post-otic nerve innervates pre-otic musculature. Furthermore, the serial homology of pre-otic and post-otic somites appears established by the fact that (5) a pre-otic somite (van Wijhe's 3d somite) is a segment of the dorsal mesoderm. That it is such seems clear, for it is defined anteriorly and posteriorly by well marked constrictions (observed by several investigators), it becomes differentiated into myotome and sclerotome, and its musculature appears first in its median wall, and becomes innervated by a ventral nerve (abducens) serially homologous with ventral spinal nerves. The fact that the primitively dorsal mesoderm of the pre-otic region grows ventrally to form the splanchnic musculature, as has been stated for Cyclostomes, Selachii, and Amphibia, is not a basis for a fundamental distinction between post-otic and pre-otic regions, since this is the method of formation of splanchnic mesoderm throughout the length of the body in Amphioxus. In this respect, as in respect to the nerves, the head shows more primitive conditions than the trunk. Since the literature of the last decade and a half shows little agreement of opinion as to the morphology of the eye-muscle nerves, more especially the oculomotorius and the trochlearis, and since in the preceding pages evidence has been given which tends to reconcile existing differences, it is important to consider briefly the bearing of their morphology upon that of the pre-otic segments. The more recent attempts to classify the eye-muscle nerves as dorsal, lateral, or ventral indicates that the point of view of morphologists is now fundamentally different from that of the older anatomists, who, in dealing with the question of the segmental value of cranial nerves, excluded the eye-muscle nerves from consideration on the ground of their inconstancy in appearance and distribution. Except on the part of Froriep, Kastschenko, and Rabl, who regard the pre-otic region as one *sui generis*, I find no tendency to revert to the view of Stannius ('49, p. 125) that "der Parallelisirung der Augenmuskelnerven mit Spinalnerven stellen sich, wegen ihrer eigenthümlichen Ursprungsverhältnisse, des ihnen zukommenden Mangels von Ganglien und der ausschliesslichen Vertheilung ihrer ungemischten Primitivröhren in den, auch ihrerseits mit Muskeln der Wirbelsäule durchaus nicht vergleichbaren, Muskeln eines Sinnes-Apparates so unüberwindliche Schwierigkeiten entgegen, dass von einer solchen nicht füglich die Rede sein kann." However, the labors of comparative anatomists, among whom may be named Huxley, Gegenbaur, M. Fürbringer, and Schwalbe, during the thirty years following the work of Stannius just quoted, resulted in so well establishing the "Bürgerrecht" of the eye-muscle nerves that morphologists now assume that they are comparable with either dorsal or else ventral segmental nerves. Only a minority of anatomists, among whom may be named Schneider ('79), van Wijhe ('82), Beard ('85), His ('88^{a}), Dohrn ('91), Neal ('96), and M. Fürbringer ('97), have regarded them as ventral segmental nerves. The weightiest well established evidence in favor of this view was first stated by His ('88), and consists in the fact that the eye-muscle nerves, at least of the adult, resemble ventral spinal nerves both in histological structure and in the situation of their motor nucleus in the ventral horn of the neural tube; and also in the less well established fact that they innervate musculature derived from segments of the dorsal mesoderm. On the other hand, the majority of morphologists, among whom may be named Balfour ('78), Marshall ('81), Dohrn ('85, '87, '90), Gaskell ('89), Hoffmann ('89, '94), Oppel ('90), Houssay ('90), Platt ('91), Froriep ('91), Zimmermann ('91), Hatschek ('92), Mitrophanow ('92, '93), and Kupffer ('94, '95, '96), while in general of the opinion that the abducens is the homologue of one or more segmental ventral nerves, have held that either the trochlearis or the oculomotorius, or both, represent dorsal (or lateral) segmental nerves. The chief arguments in favor of this view consist in evidence (1) of the development of these nerves from neural-crest cells; (2) of a cellular or so called ganglionic structure of the nerves in the embryo; (3) of transitory or permanent ganglia in connection with them; and (4) of the development of at least a part of the musculature innervated by them from splanchnic mesoderm. Thus there is to-day a distinct conflict as to the morphology of the eye-muscle nerves, one party to the conflict being supported by histological evidence, the other by embryological. The assumption by His ('88), that the eye-muscle nerves develop as processes of medullary cells (neuroblasts), — which is involved in his contention that they are the serial homologues of ventral spinal nerves, — has never hitherto received the requisite embryological confirmation. In fact, the latest embryological evidence concerning the development of the oculomotorius and trochlearis seems quite irreconcilable with the view of Schneider ('79), van Wijhe, and His. In regard to the latter nerve, Hoffmann ('89, p. 338) says, if one disregards the fact that no ectodermal fusion takes place, "so gleicht die Anlage des Trochlearis in sehr jungen Entwicklungsstadien [of Lacerta] vollkommen der eines segmentalen Kopfnerven, besonders der des Trigeminus." Froriep also finds that the trochlearis possesses in early stages a ganglion, and is differentiated from neural-crest cells *in situ*. Miss Platt ('91^a, p. 259) likewise states that "in Acanthias the development of the trochlearis in all essential respects so completely corresponds to that of the trigeminus and facialis, that like them it must be considered to combine primarily those dorsal and ventral elements which have separate roots in the nerves of the trunk. It can, therefore, not be regarded as the ventral root of another segmental nerve." Moreover, Kupffer ('95, '96) finds the trochlearis to possess in Ammocœtes both dorsal and ventral roots.

With regard to the oculomotorius, the conclusions of embryologists are even more conflicting. While Dohrn ('91) finds that this nerve is formed by the migration of cells from the ventral wall of the midbrain, and considers it a motor nerve, Miss Platt ('91^a) states that she has shown the oculomotorius to be "undoubtedly originally sensory." Her observation that the nerve develops from the ganglion toward the brain has been confirmed by both Mitrophanow ('93) and Sedgwick ('95). Nevertheless the evidence which has been stated by me in division VI. shows conclusively, as I believe, that all the eye-muscle nerves, oculomotorius, trochlearis, and abducens, develop, like ventral spinal nerves, as processes from neuroblasts lying in the ventral horn of the medullary tube. Therefore, from their development, as well as their adult histological structure and relationships, the eye-muscle nerves must be regarded as the serial homologues of ventral spinal nerves. Finally, with the accumulating evidence given by many investigators, — among them Beard, Dohrn, Ayers, and Kupffer, — that the complicated sensory organs of ear, eye, and nose are differentiations of lateral-line sense organs, we may conclude that there exist no fundamental differences in *nature* between pre-otic and post-otic segments.

The *number* of cephalic segments in the post-otic region (Sewertzoff, Fürbringer) appears to be variable in different Vertebrates. If the estimate given by Hoffmann ('94) for Squalus be correct, there are six post-otic cephalic segments in that form. In the otic and pre-otic regions, I hold the number to be not greater than six,[1] and the exact numerical correspondence of neuromeres and somites very strongly supports the estimate of six, which accords very closely with that made, upon similar but not identical grounds, by van Wijhe, Beard, Marshall, and Miss Platt. I cannot agree with Hoffmann ('96) and M. Fürbringer ('97), who — from the evidence that there is one more mesodermal segment (viz. the "anterior") in Squalus and Galeus than in other known Selachian embryos — conclude that still other anterior mesodermal segments have phylogenetically disappeared, and that it is therefore impossible for us to estimate the number of pre-otic segments. *We have quite as little reason to believe that somites anterior to Platt's have disappeared, as we have to believe that encephalomeres anterior to encephalomere I (the primary forebrain) have once existed.* In the exact numerical correspondence of neuromeres and somites we have, not only evidence of the serial homology of head and trunk segments, but the means to determine their number in the pre-otic region.

IX. Summary.

I am unable to regard Locy's "neural segments" as segments in the true sense of the word, because I find them irregular in size, inconstant in number, bilaterally asymmetrical, and without definite relation to structures known to be segmental. They are phenomena connected with the proliferation and disassociation of the cells of the neural crest.

The posterior boundary of the cephalic plate coincides with the posterior boundary of encephalomere VI, opposite which the auditory invagination takes place.

Orr's criteria for hindbrain neuromeres hold good only for the later stages of development of S. acanthias. In the early stages of this animal, the neuromeres are local thickenings of the lateral zones, as well as dilatations of all of the zones of the medulla. As paired glangionic enlargements of the central nervous system, they obviously resemble, except in position, the ventral chain of ganglia of Annelids. Therefore they cannot be explained as the passive result of mechanical shoving or bending. The constrictions between the neuromeres, as well as the crowding of nuclei in the regions of constriction, may however be, and most probably are, intensified by shoving or bending of the neural tube.

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[1] Six neuromeres alternating with five somites. With Miss Platt ('94) I hold that the otic sense organ was primitively situated above the constriction between van Wijhe's 4th and 5th somites.

No structural conditions are presented by the myelomeres which are not reconcilable with the hypothesis that their existence is dependent upon the presence of the mesodermal somites. If they ever possessed a dorsal segmentation like that of the "hindbrain neuromeres," — and there is no evidence to show that they ever did, — it has been lost. But, though they appear of doubtful morphological value, their numerical correspondence with nerves and somites attests their metameric value.

The so called neuromeres of the forebrain and midbrain (encephalomeres of Zimmermann) are not morphologically comparable with "hindbrain neuromeres," since they are simply dorsal or ventral expansions which are secondary in the time of their appearance. I hold that there are much better reasons — viz. on the grounds of time of appearance, of structure, and of relation to nerves and somites — for regarding each of the primary forebrain and midbrain vesicles (neuromeres I and II) as serially homologous with hindbrain neuromeres (neuromeres III to VII), than for so regarding their later subdivisions. The latter are cœnogenetic vesiculations of the neural tube, and not of metameric value.

Both dorsal ganglia and ventral nerves in the trunk develop in the regions of constriction between myelomeres. A comparison with the conditions in Amphioxus and Petromyzon shows that this condition is not to be regarded as primitive, but that previously dorsal and ventral nerves alternated, the former being intersomitic in position. Such topographical relation is retained by some cranial nerves, viz. V, VII, IX, and X (Urvagus).

The ganglionic Anlagen of four cranial nerves, viz. V, VII, IX, and X, are proliferated from four encephalomeres, viz. III, V, VI, and VII. Chiefly for this reason, but also because of the clear connection of two splanchnic motor roots, viz. V and VII, with two of the encephalomeres, I conclude that the primitive metameric relations of the latter were with the visceral arches. The local thickenings of the hindbrain neuromeres (encephalomeres) may be considered as the primitive nervous centres of nerves which corresponded numerically with visceral arches. If they were such, then one of the encephalomeres (IV) affords evidence of a lost visceral arch.

Although the structure of myelomeres and encephalomeres is seen to be different, yet in the stages of embryonic development, where both are present, the latter are seen to have segmental value from the fact that corresponding with them there is an equal number of somites. These somites, as exemplified in the 3d (van Wijhe's), are morphologically comparable and serially homologous with trunk somites. I conclude, then, that there was a primitive correspondence between neuromerism, mesomerism, and branchiomerism.

The development, histological structure, and relationships of the eye-muscle nerves (III, IV, and VI) show them to be the serial homologues of ventral spinal nerves. Like the latter (His), they develop as axis-cylinder processes of neuroblasts in the ventral horn of the neural tube.

Pre-otic and post-otic metameres, like their integral parts, are serially homologous with one another. Therefore, if the latter are serially homologous with trunk metameres the former must be also. Table III. (p. 253) summarizes my opinion as to the primitive composition of metameres I to VII. I regard the r. opthalmicus profundus as a segmental dorsal nerve belonging to metamere II, while the oculomotorius is its ventral root. The trochlearis is the ventral nerve of metamere III, and the abducens represents the ventral nerves of metameres IV to VII.

There are five mesomeres alternating with six neuromeres in the otic and pre-otic regions of the Vertebrate head. Probably eleven neuromeres are finally included in the head of Squalus. The evidence of the numerical correspondence of neuromeres and mesomeres shows that there is no more reason for believing that somites have been lost anterior to Platt's (anterior) somite, than that neuromeres have been lost anterior to the primary forebrain.

In agreement with van Wijhe, I homologize the mouth of Amphioxus with the left half of the mouth of Craniota. The first pair of permanent visceral clefts in Amphioxus are exactly homologous with the hyomandibular clefts of higher Vertebrates. The eight visceral clefts possessed by Amphioxus at its "critical stage" (Willey) are exactly homologous with the eight morphological clefts found in some Selachii and Cyclostomes.

This investigation has been made in the Zoölogical Laboratory of the Museum of Comparative Zoölogy at Harvard College. I gratefully acknowledge the valuable assistance and advice of its Director, Prof. E. L. Mark, at whose suggestion the work was undertaken. I am indebted to Alexander Agassiz for the privilege of studying at his private laboratory in Newport; also to Professor Mark for embryonic material of Petromyzon, and to Miss Julia B. Platt for embryonic material of Amphioxus.

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DESCRIPTION OF PLATES.

All the drawings were made with the Abbé camera lucida. Figure 40 (Plate 6) is, however, a reconstruction from sections and dissected specimens. The Figures of Plates 8 and 9, with the exception of Figures 61 and 65, are also reconstructions from several sections. In sagittal sections, the embryo is always viewed from the right side. In cross sections, it is the posterior face of the section that is shown, so that right in the figure corresponds to right in the section. In frontal sections, the dorsal face is shown, so that right in the figure here also corresponds with right in the section. Only Figures 2 and 3 (Plate 1) represent embryos viewed from the ventral side, so that what appears on the left side in these two figures is really on the right side of the embryo. The cells of the neural crest are in all cases colored blue.

ABBREVIATIONS COMMON TO ALL FIGURES OF TEXT AND PLATES.

*	Posterior limit of cephalic plate.
I–VII.	Encephalomeres.
1–7.	Somites (van Wijhe's).
2′, 3′.	Cavities of head somites 2, 3.
V. md.	Ramus mandibularis trigemini.
V. mx.	R. maxillaris trigemini.
V. opt. su.	R. ophth. superficialis trigemini.
V. opt. p'fnd.	R. opth. profundus trig.
V. rx. maj.	Radix major trigemini.
V. rx. min.	“ minor trigemini.
VII. ac.	Ramus acusticus facialis.
VII. buc.	“ buccalis “
VII. hoi.	“ hyoideus “
VII. opt. su.	“ ophth. superficialis fac.
a, β, γ.	Position of frontal sections (Figs. 36, 37, 38).
aβ.	(Fig. C.) Position of section (Fig. D).
a.	“Anterior cavity” (Figs. B, C, E). Ventral fibre tract (Fig. F).
abd.	Abducens nerve.
ao. d.	Dorsal aorta.
arc. vsc. 1.	Visceral arch 1.
ar'ent.	Archenteron.
au.	Auditory invagination (otic vesicle).
ax-cyl.	Axis-cylinder process.
brs. vsc. 1–6.	Visceral pouches 1 to 6.
cav. a.	Platt's somite (anterior cavity).
cbl.	Anlage of cerebellum.
cd.	Chorda dorsalis.
cl. crs. n.	Neural-crest cells.
cl. ms-ce.	Cells of mesocephalic ganglion.
cl. n'bl.	Neuroblastic cell.
coms. a.	Anterior commissure.
coms. d.	Dorsal “
coms. p.	Posterior commissure.
coms. su.	Superior “
ec'drm.	Ectoderm.
en'drm.	Entoderm.
ent.	Entoderm.
fis. vsc. 1–6.	Visceral clefts 1 to 6.
gls-phy.	Glossopharyngeus nerve.
gn. ac-fac.	Ganglionic Anlage of acustico-facialis.
gn. fac.	Ganglion of acustico-facialis.
gn. Gas.	Gasserian ganglion.
gn. gls-phy.	Ganglion of glossopharyngeus.
gn. ms-ce.	Mesocephalic ganglion.
gn. trig.	Ganglionic Anlage of the trigeminus nerve.
gn. spi.	Spinal ganglion.
gn. vag.	Ganglionic Anlage of the Vagus.
i'fb.	Infundibulum.
la. ct.	Lamina cutis (cutis plate).
la. mu.	Lamina muscularis (muscle plate).
m-b.	Midbrain.
mu. ob. su.	Superior oblique muscle.
mu. rt. su.	“ rectus muscle.
mu. rt. a.	Anterior rectus muscle.
my'cœl.	Myocœle.
myl-mer.	Myelomere.
my-tm.	Myotome.
n-po.	Neuropore.
oc-mot.	Oculomotorius nerve.
pr'enc.	Prosencephalon.
rx. v.	Ventral root of nerve.
so.	Somite.
tb. n.	Neural tube.
thl.	Thalamic portion of the trigeminus Anlage.
trch.	Trochlearis nerve.
vag.	Vagus nerve.
vn. crd.	Vena cardinalis.
vs. opt.	Optic vesicle.

PLATE 1.

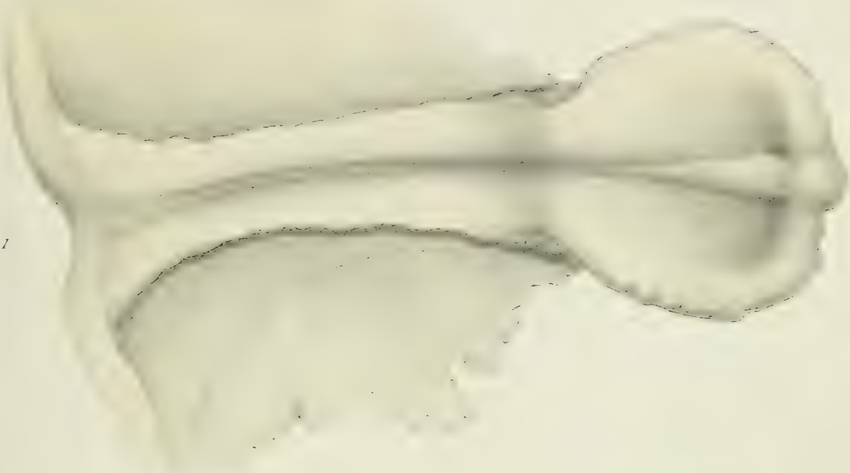
All figures magnified 43 diameters, and oriented on the plate with the chief axis horizontal, the anterior end of the embryo to the right. The embryo made translucent was drawn in outline with camera lucida and afterwards studied as an opaque object.

Fig. 1. A dorsal view of an embryo with 6 to 6½ somites. The edges of the neural plate are seen to be irregularly lobed. The two deep depressions at the anterior end of the cephalic plate mark the position of the future fundus of the infundibulum.

Fig. 2. A ventral view of the same embryo. Locy's segments are seen as lobings of the ventrally recurved margin of the neural plate.

Fig. 3. A ventral view of another embryo of the same stage of development. The specimen was dissected to show the chorda, a rod in the median axial line, on either side of which lie the somites, van Wijhe's seventh somite being designated as 7. An asterisk (*) marks the posterior boundary of the cephalic plate.

1



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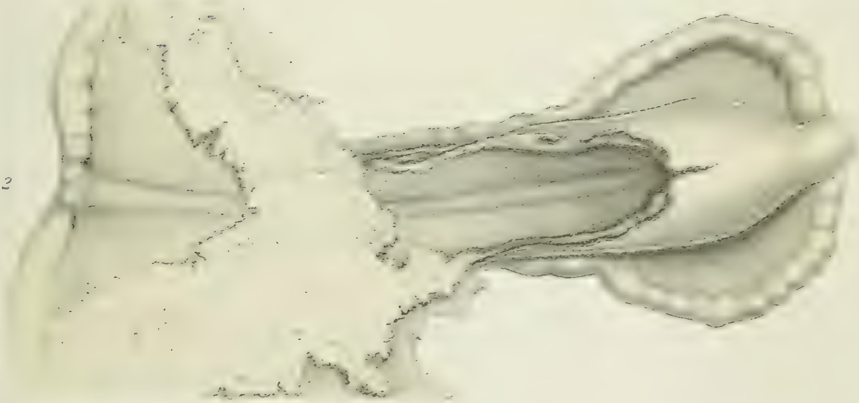

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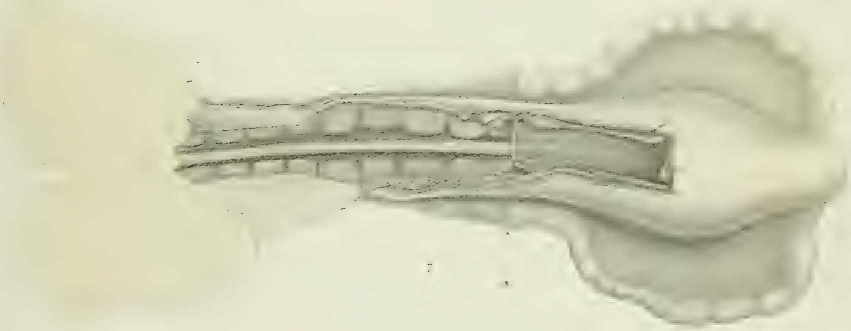


H. V. Neal del.

E. Meisel lith Boston

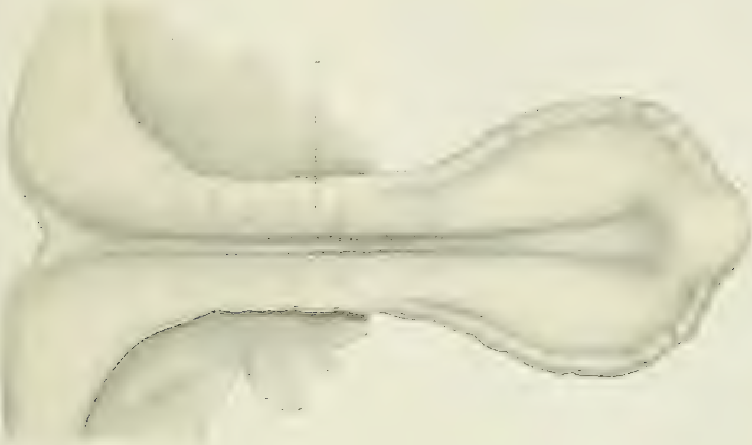
PLATE 2.

All figures magnified 43 diameters and oriented as in Plate 1. The outlines were first made from the translucent embryos with camera lucida, and afterwards the embryos were studied as opaque objects.

Fig. 4. An embryo with 4 somites viewed from the dorsal side. Locy's segments are seen to be confined to the "marginal bands" of the cephalic plate.

Fig. 5. An embryo with 10 or 11 somites viewed from the right side and partly from above. The posterior part of the cephalic plate is seen to be sharply flexed ventrad on the right side.

Fig. 6. An embryo with 12 somites viewed from the right side. The neural folds in the region of the cephalic plate have not yet met in the mid-dorsal line. The demarcation between cephalic plate and trunk is seen to be sharp. The anterior three primary vesicles (encephalomeres I, II, and III) appear in surface study as shown in the figure. In neither this embryo nor in the one represented in Figure 5 do Locy's segments appear.



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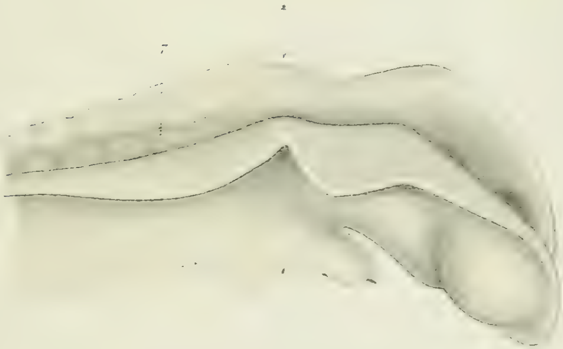

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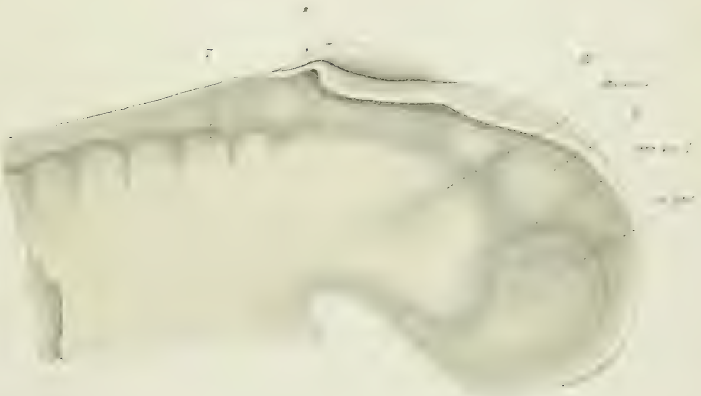


H.V.Neal del.

B. Meisel lith Boston

PLATE 3.

All figures drawn from cleared specimens and magnified 43 diameters. The neural tube seen in optical sagittal section. Neural-crest cells (ganglionic Anlagen) colored in blue. In all cases the embryo is viewed from the right side.

Fig. 7. An embryo with 14 to 16 somites. Six vesicles only appear, and these are included within the limits of the cephalic plate. Neural crest (trigeminus Anlage) differentiated in the region of encephalomeres II and III. The mesodermic constrictions dividing somites 1, 2, 3, and 4 have appeared. Two visceral pouches (1 and 2) are in the process of breaking through the lateral plates (splanchnic mesoderm).

Fig. 8. Embryo with 18 or 19 somites. A thickening of the lateral zones in the posterior part of encephalomere III (not shown in figure) appears in sections of this stage. The acustico-facialis Anlage has become differentiated in the region of encephalomere V. The "anterior cavity" (Platt's) begins to be cut off from the mesoderm of the 1st somite (van Wijhe's).

Fig. 9. Embryo with 19 or 20 somites. A dorsal expansion now appears behind VI, as the first indication of encephalomere VII. Posteriorly it is bounded by somite 6. The constriction between van Wijhe's 3d and 4th somites has become obscured by the migration of cells from both sides of the constriction to meet the advancing Anlage of the acustico-facialis.

Fig. 10. Embryo with 21 or 22 somites. The conditions remain practically unchanged.

Fig. 11. Embryo with 24 or 25 somites. A ventral migration of neural-crest cells in the region of encephalomere VI has now begun, and the crest is now differentiated in the region of encephalomere VII and posteriorly.

Fig. 12. Embryo with 26 or 27 somites. A continuous neural crest extends from encephalomere V into the trunk region. Thalamic portion of the trigeminus Anlage clearly differentiated.

Fig. 13. Embryo with 28 to 30 somites. At this stage all of van Wijhe's somites appear clearly differentiated. The Anlagen of the acustico-facialis and the glossopharyngeus, differentiated from encephalomeres V and VI, appear topographically related to the constrictions between van Wijhe's somites, 3–4 and 4–5.

Fig. 14. Embryo with 33 or 34 somites. Trochlear portion of trigeminus Anlage (compare Fig. 21, *trch.*) clearly differentiated. The commissure connecting acustico-facialis and glossopharyngeus appears dorsal to the auditory invagination.

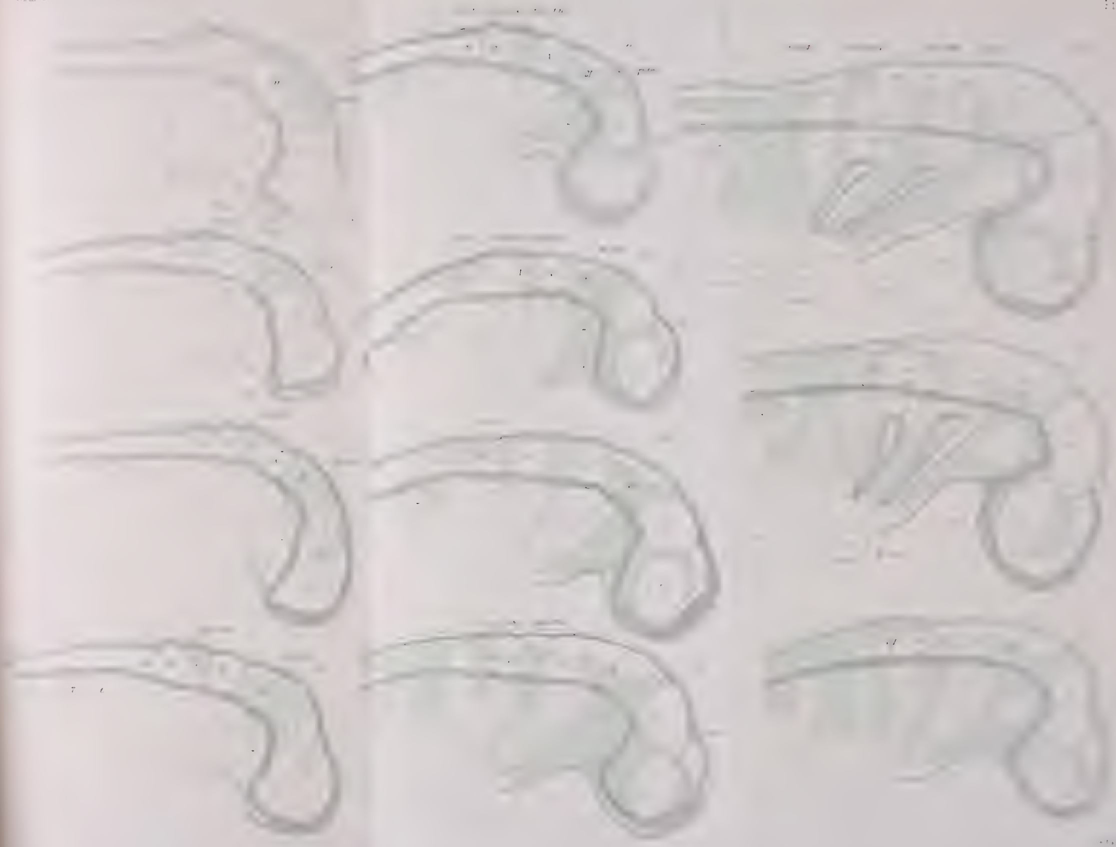
Fig. 15. Embryo with 38 or 39 somites.

Fig. 16. Embryo with 42 somites. Platt's "anterior somite" (*cav. a.*) clearly differentiated. The anterior cells of the vagus Anlage, proliferated from encephalomere VII, have become clearly differentiated in the 3d visceral arch as the Urvagus Anlage. Two visceral clefts have appeared.

Fig. 17. Embryo with 48 somites (7.5 mm.). The fifth and seventh nerves have assumed fibrillar relation with the neural tube. The main branches of the trigeminus begin to appear.

NEAL-NERVOUS SYSTEM SQUALUS

PLATE 3.



H.V.N. del.

PLATE 4.

Figs. 18 and 21 magnified 23 diameters. Figs. 19 and 20 magnified 21 diameters.

Fig. 18. An embryo with 52 somites (8 mm.). The otic capsüle now lies opposite encephalomere VII. The thalamic and trochlear portions of the trigeminus appear only as scattered clumps of cells. Posterior commissure clearly differentiated. Between this and the preceding stage the oculomotorius has appeared as a fibrillar process from the ventral wall of the midbrain, near *gn. ms-ce.*

Fig. 19. An embryo with 65 somites (10 mm.). The chief peripheral branches of the cranial nerves have appeared; the abducens, as a process from the ventral wall of encephalomere VII.

Fig. 20. An embryo with 78 to 80 somites (16 or 17 mm.). In this stage the ramus opthalmicus superficialis trigemini appears to have fibrillar relation with the mesoderm of the 2d somite, which is growing forward. The fibrous process of the abducens has come into relation with the 3d somite, and also is seen to have a branch passing to the mesoderm posterior to its place of origin. Most of the fibres of the ramus mandibularis trigemini appear in connection with encephalomere III.

Fig. 21. An embryo 21 or 22 mm. long. The trochlearis is now differentiated, and in relation with the musc. obliquus posterior.

E. Weise, lith. Berlin

PLATE 5.

All the Figures except 31 and 32 represent frontal sections of embryos viewed from the dorsal side. All except Figures 25, 32, and 35 are magnified 43 diameters.

Fig. 22. A frontal section of an embryo with 14 or 15 somites. Encephalomere IV appears as a thickening of the lateral walls of the neural tube. No local thickening seen in the region of encephalomere III.

Fig. 23. From an embryo with 16 or 17 somites. A local thickening of the lateral walls in the posterior part of encephalomere III appears.

Fig. 24. From an embryo with 19 or 20 somites. The first four hindbrain neuromeres are now seen as local thickenings of the lateral walls, the thickening of neuromere III affecting its posterior part only.

Fig. 25. From an embryo with 28 to 30 somites, magnified 75 diameters. Five hindbrain neuromeres are seen. The auditory invagination appears opposite encephalomere VI.

Fig. 26. From an embryo with 50 somites (8 mm.) in the region of the "Deckplatte," showing the faintly marked expansions of the encephalomeres.

Fig. 27. A more ventral section of the same embryo. The encephalomeres sharply defined by constrictions. A secondary constriction in encephalomere III appears.

Fig. 28. A more ventral section of the same series, in the region of the lateral zones. The local thickenings of the encephalomeres well marked.

Fig. 29. A still more ventral section of the same embryo. The inner cusps between the neuromeres appear as in the more dorsal sections (Fig. 27).

Fig. 30. Frontal section in the region of the lateral zones of an embryo of 15 mm. The structure of the neuromeres is seen to be the same as that described by Orr ('87) for the Lizard.

Fig. 31. Cross section of an embryo with 20 somites, in the region of encephalomere IV, to show the thickening of the lateral zones.

Fig. 32. Cross section of an embryo with 28 to 30 somites in the posterior region of encephalomere III. The lateral zones more markedly thickened than in the previous stage (Fig. 31).

Fig. 33. Frontal section of an embryo with 50 somites (8 mm.), killed with a mixture of chromic, picric, and sulphuric acids, showing great intensification of the neuromeres, as the result of contraction due to inadequate fixation. The drawing, however, exaggerates the phenomena, since it represents the nuclear regions of the medullary wall with deeper shading.

Fig. 34. Frontal section of a 19-day *Swine* embryo. The constrictions between the neuromeres are sharply defined.

Fig. 35. Frontal section of an embryo of *Amblystoma* shortly after the closure of the neural tube. The neural tube is sharply outpocketed in the regions of proliferation of the ganglionic Anlagen of nerves V and VII. No evidence of a thickening or outpocketing comparable with encephalomere IV appears either at this or later stages.

PLATE 6.

All Figures, except 40, magnified 100 diameters. Only the *right* half of the embryo is shown in Figures 36–39, 42, and 44.

Fig. 36. Frontal section of an embryo with 28 to 30 somites, showing the structure of the neuromeres IV and V in the region of the "Deckplatte."

Fig. 37. A more ventral frontal section in the same series cut in the region of the lateral zones. The neuromeres appear as well marked local thickenings. The radial arrangement of nuclei much less clearly shown than in the preceding section (Fig. 36).

Fig. 38. A still more ventral section of the same series, in the region of the "Grundplatte." The inner concavity appears as in the dorsal section (Fig. 36).

Fig. 39. Frontal section of an embryo with 28 to 30 somites, in the region of the trunk, showing the structure of the myelomeres and their relation to the somites.

Fig. 40. A reconstruction from sections and dissected specimens of the anterior end of an embryo with 28 to 30 somites, magnified 56 diameters. The lumen of the neural tube is exposed so as to show the hindbrain neuromere as local thickenings of the left wall. Van Wijhe's somites, at this stage separated by clearly marked constrictions, and Platt's anterior somite, are seen. Cells, in chief part derived from the neural crest, are seen surrounding the mesodermic epithelium of the 1st and 2d visceral arches.

Fig. 41. A cross section of an embryo with 28 to 30 somites in the trunk region. It is seen that the somites press against the ventral half of the neural tube. A migration of mesenchymatous cells from the sclerotome portion of the somite has already begun.

Fig. 42. Frontal section of an embryo with 50 somites (8 mm.) in the trunk region (ectoderm omitted), taken in the region of the points of exit of the ventral nerves. No constrictions in the ventral wall of the neural tube are to be seen at this stage, but the ventral nerves lie opposite the middle of the somites.

Fig. 43. A more dorsal frontal section from the same series as Figure 42. Constrictions in the lateral wall, opposite which the ganglia lie, show no corresponding ridges on the inner surface of the lateral wall.

PLATE 7.

Figures 44 to 53 illustrate the primary and secondary subdivisions of the forebrain and midbrain (encephalomeres I and II). All the Figures, except 47, 48, 53, 55, and 56, magnified 43 diameters.

Fig. 44. A parasagittal section of a *Chick* embryo of 33 hours' incubation (14 somites). Seven primary expansions of the encephalon appear, from the fifth of which, as in Squalus, the Anlage of the acustico-facialis is proliferated.

Fig. 45. A parasagittal section of a Squalus embryo with 18 somites. Six primary vesiculations (encephalomeres) are seen, all included in the region of the cephalic plate. Clefts in the dorsal mesoderm separate from each other all of van Wijhe's somites except the 4th and 5th.

Fig. 46. A parasagittal section of a Squalus embryo with 28 to 30 somites. Both encephalomeres II and III have become subdivided by constrictions, that of the former, however, affecting the ventral wall only. All of van Wijhe's somites separated by clearly marked mesodermic clefts.

Fig. 47. A parasagittal section of an embryo with 65 somites, magnified 23 diameters. Two subdivisions of encephalomeres I and three subdivisions of encephalomere II appear. The latter remains, however, dorsally a simple expansion. Nerve relation of encephalomeres II and VII with somites 1 and 3 shown.

Fig. 48. A frontal section in the dorsal part of encephalomeres I and II of an embryo with 30 to 32 somites, magnified 56 diameters. Only two vesiculations appear. Relation of thalamic portion of the trigeminus Anlage to these shown.

Fig. 49. Frontal section in the dorsal portion of encephalomeres I and II in an embryo with 19 or 20 somites. Two vesiculations only appear.

Fig. 50. A frontal section of the same embryo as that shown in Figure 48, but more ventral, showing the constriction in the ventral wall of the midbrain.

Fig. 51. A frontal section of an embryo with 65 somites in the dorsal part of encephalomeres I and II (forebrain and midbrain), showing subdivision (thalamic) of the former.

Fig. 52. A more ventral frontal section in the same series, showing a constriction in the lateral wall of the midbrain corresponding in position with the posterior commissure (*coms. p.*). The constriction in the forebrain corresponds with the superior commissure.

Fig. 53. A frontal section, showing forebrain and midbrain regions in an embryo of 22 mm., magnified 23 diameters. Two constrictions only appear, one in the region of the superior commissure, and the other in the region of the posterior commissure.

Fig. 54. A cross section of an embryo with 6 or 7 somites in the region of the cephalic plate, showing the ventral flexure of its edges.

Fig. 55. A cross section of an embryo at a stage when the edges of the neural plate are about to be raised, showing the differentiation of a neural crest in the anterior part of the cephalic plate. Magnified 100 diameters.

Fig. 56. A cross section in the posterior part of the cephalic plate of an embryo with 9 or 10 somites, showing that migration of neural-crest cells has already begun. Magnified 85 diameters.

PLATE 8.

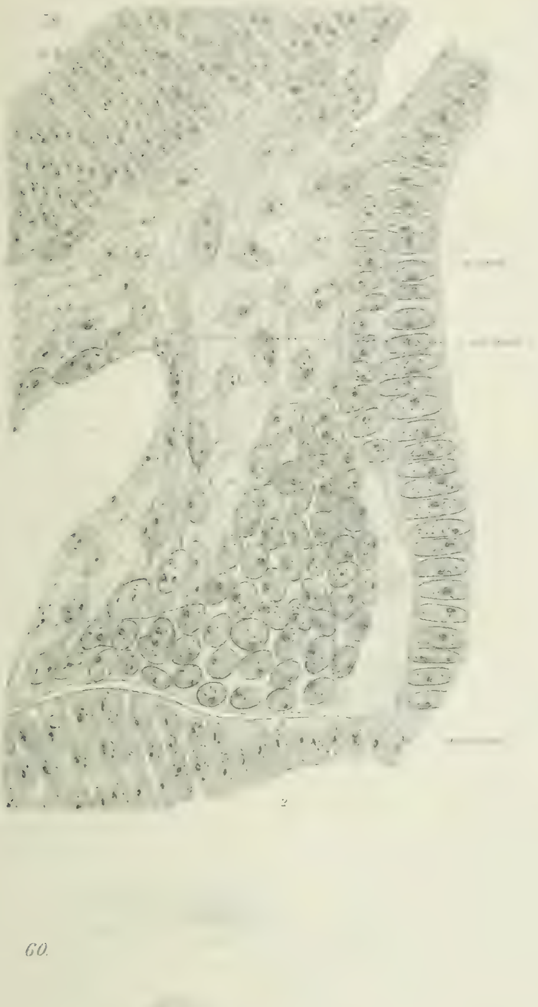
Stages in the development of the nerves oculomotorius, ramus ophthalmicus superficialis trigemini, and ramus ophthalmicus profundus trigemini.

Fig. 58. A frontal section of an embryo with 55 somites ($8\frac{1}{2}$–9 mm.). Embryo killed with Davidoff's fluid. The oculomotorius appears as a cellular strand extending from the inner side of the mesocephalic (profundus) ganglion to the wall of the midbrain. Magnified 500 diameters. Reconstructed from three sections.

Fig. 59. A sagittal section of an embryo with 56 somites. Embryo killed with Davidoff's fluid. Near the brain the nerve appears composed of loose fibrillæ, while peripherally it is cellular in appearance. Magnified 360 diameters. Reconstructed from five sections.

Fig. 60. A combination of two parasagittal sections through the left side of an embryo of 16 mm. Protoplasmic processes from the ramus ophth. sup. trig. appear in relation with the anterior projection of the 2d cavity (musc. obl. superior). Magnified 70 diameters.

Fig. 61. A parasagittal section from the right side of an embryo with 51 or 52 somites (8 mm.). A well marked fibril passes from the mesocephalic ganglion to van Wijhe's 1st somite. The oculomotorius has not yet appeared.



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H.V.Neal del.

P. Meisel Lith Boston

PLATE 9.

Stages in the development of the abducens nerve. All the specimens were killed with Davidoff's fluid (corrosive-acetic). All Figures are from frontal sections except Figure 65.

Fig. 62. A frontal section of an embryo with 62 somites (9 mm.). Magnified 450 diameters. Two roots are present.

Fig. 63. From an embryo with 68 somites (10 mm.) magnified 285 diameters. The course of the nerve is very direct in this stage, at least in the specimen figured. Throughout the most of its course it is entirely free from nuclei.

Fig. 64. A combination from 7 sections of an embryo with 80 somites. Three roots present on the side of the embryo figured. Deeply staining nuclei appear in close connection with the nerve, and there is some (in my opinion doubtful) evidence of the migration of nuclei to or from the neural tube. Peripherally the nerve divides into fine fibrillæ. Magnified 200 diameters.

Fig. 65. A cross section of an embryo with 75 somites in the region of the posterior root of the abducens, magnified 285 diameters. Evidence of migration of nuclei (?).

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